PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

FOURTH SERIES

Vol. XXXI, No. 15, pp. 369–416; 1 fig. September 10, 1963

REMARKS ON THE ZOOGEOGRAPHY OF PHILIPPINE TERRESTRIAL SNAKES

By

Alan E. Leviton

California Academy of Sciences, San Francisco 18,
and *Division of Systematic Biology, Stanford University*

For more than thirty years interest in the Philippine herpetofauna lay dormant, a reawakening taking place within the past ten years as evidenced by the studies of Alcala (1962), Brown (1955–1962), Inger (1954), and the writer (1952–1962). The last studied the Philippine snakes, and as an outgrowth of that work re-evaluated the zoogeographic relations of the Philippine Islands on the basis of the distribution of these animals. Partial results of the systematic study are in press, and additional parts are in preparation. The present paper, therefore, incorporates results of as yet unpublished studies. Nomenclatural problems, especially name changes, presented in this paper are fully explained in the series now in press.

The writer is in debt to many people for their aid, especially for the loan of specimens for study. Their assistance is acknowledged elsewhere. For interest in and criticism of the present paper the writer is most especially indebted to Dr. George S. Myers of the Division of Systematic Biology, Stanford University, under whose sponsorship the original work was carried out. To Dr. Walter C. Brown of Menlo College, Menlo Park, California, who has been active in the Philippines since 1954, and Mr. Angel C. Alcala, Silliman University, Dumaguete, Philippines, the author wishes to express his thanks for permission to study collections they amassed in those islands between 1954 and 1959 and to include several of their new records in this

paper (those species whose names are preceded by an asterisk [*]). Dr. Brown has papers in manuscript that deal with the zoogeography of several of the islands, particularly Negros, Bohol, and Palawan, in far more detail than they are treated here.

This study was supported in part by a grant, in 1960, from the Penrose Fund of the American Philosophical Society.

INTRODUCTION

The zoogeographic relations of the Philippine Islands were discussed in considerable detail by Dickerson, and others, in 1928. Dickerson (1941), Mayr (1944), Myers (1951), Inger (1954), and Darlington (1958) have contributed additional material to the subject.

The present discussion is confined, insofar as that is possible and reasonable, to an analysis of the snake fauna. Several factors have dictated this approach. For one, I am thoroughly familiar with the systematics of only one group of Philippine animals. Inasmuch as the quality of one's zoogeographic conclusions depends on the correctness of the proposed systematic relationships of the animals involved, at least in large part, I am not in a position to render judgments regarding the probable zoogeographic relationships of animals I know little or nothing about. Secondly, I see no reason to repeat what has already been written regarding the distribution of other groups of animals. On the whole, the conclusions reached here do not differ markedly from those expressed more than thirty years ago by Dickerson and the authors who collaborated with him.

No attempt is made here to outline the geological history of the Philippine Islands. Dickerson (1924 and 1928b), Corby (1951), and Irving (1952) have already prepared such reviews, and much Philippine geology was incorporated into the works of van Bemmelen (1949) and Umbgrove (1938). Inger (1954) summarized the geological history of the Philippines in the introduction to his discussion on amphibian zoogeography. The work of Smith (1924) has been drawn upon for geological data on some of the small, obscure islands in the Philippines which are infrequently mentioned by others.

One point regarding the interrelationship between Philippine geology and the distribution of snakes in that region should be noted at this time. It is reasonably certain that the modern snake fauna of the Philippine Islands is a post-Miocene phenomenon. There is no evidence to indicate that Miocene and pre-Miocene Asian fauna could have entered the Philippines, most of the islands at that time being covered by shallow seas. However, periodic transgressions and regressions of the shallow inland seas during the Pleistocene, and the concomitant exposure of greater land masses, most profoundly affected the modern Philippine snake fauna, and I have drawn frequent attention to this matter.

GEOGRAPHICAL POSITION OF THE PHILIPPINE ISLANDS

The Philippine Islands comprise a group of some 7,100 islands, islets, and rocky crags, of which no more than 462 have areas greater than that of

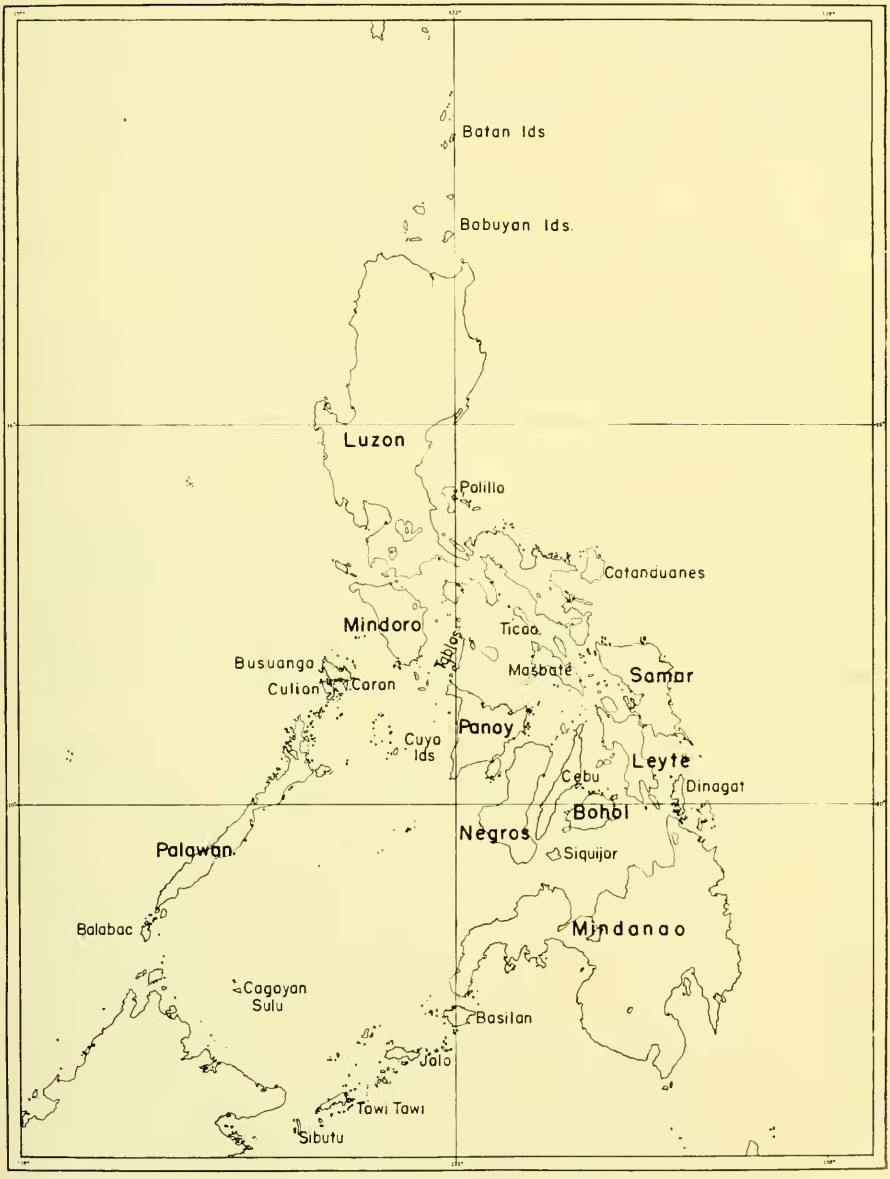

Figure 1. The Philippine Islands.

one square mile. The political boundaries of the Philippine Islands extend from Sibutu Island [4° 40′ N. Lat.] on the south to Y'Ami Island [21° 05′ N. Lat.] on the north side of the Bashi Channel, and from 116° 50′ to 136° 35′ E. Longitude. The eastern border of the archipelago is formed by the Mindanao Trench, which attains depths in excess of 35,000 feet. On the south is the Celebes Sea and the partially enclosed Sulu Sea, both of which reach depths in excess of 12,000 feet. The southern and northern portions of the China Sea, which forms the west flank of the Philippines, are shallow; however, depths in excess of 7,000 feet are reached off the west coast of Luzon Island.

There are eleven islands in the archipelago having areas of greater than 1,000 square miles. It has been estimated that there is a total of 114,830 square miles of subaerial land in the Philippines, 68 per cent of which is incorporated into the two islands of Luzon (40,814 square miles) and Mindanao (36,906 square miles).

The islands are mountainous, especially parts of Luzon, Mindanao, Mindoro, Negros, Palawan, and Panay, and elevations of 4,500 feet and more are not uncommon. All the principal peaks are volcanic in origin. However, some mountain ranges of folded sedimentary rocks have been identified, especially in a north-south belt extending through the central part of the archipelago.

Shallow submarine platforms (usually less than 50 meters below the surface) join many of the islands. These platforms and their attendant islands must have formed larger land masses during the Pleistocene when sea level was sufficiently lowered to expose them to subaerial erosion. The most prominent of these platforms include the Palawan shelf, the Sulu platform, the Mindanao platform, the western Visayan shelf, and the Camarines [= Luzon] platform.

Island connections have been altered, both in past and in the present, by block-faulting. Consequently, it is frequently difficult to determine whether several islands have been connected except by inferences based upon comparison of faunal elements.

The Philippine Islands are, according to Darlington (1957, p. 500), a fringing archipelago (*i.e.*, islands which have not been recently joined to nearby continental masses, but which nevertheless have received "fringes" of continental faunas). Many authors have partitioned the Philippines between two faunal regions. The southern islands of the Sulu and Palawan archipelagos have been assigned to the Oriental Region, while the northern islands have been placed in a transitional region which lies between the Oriental and Australian regions (Huxley, 1868; Dickerson, *et alii*, 1928). More recently, Mayr (1944) has assigned the entire Philippine Archipelago to the Oriental Region, while Inger (1954) suggests that the islands of the

Palawan chain "may be set off from the remainder of the archipelago by virtue of the absence of Papuan genera." There are few Papuan elements in the Philippine fauna, and those which have entered the islands probably did so by fortuitous means. On the other hand, the Malayan elements in the Philippines dominate the fauna, albeit they are neither so numerous nor so diversified as they are in western Indonesia and the Malay Peninsula. Furthermore, the Philippines do not represent a transitional region through which faunal elements are able to pass from one major faunal region to another, but rather the islands form a "dead-end street." Consequently, I am inclined to agree with Mayr and believe that the Philippines should be included within the Oriental Region.

COMPOSITION OF THE TERRESTRIAL PHILIPPINE SNAKE FAUNA

All but two families of Asian snakes have been reported from the Philippines. The two exceptions include the members of the family Uropeltidae, which are confined to Peninsular India, and those of the family Aniliidae, a single species of which enters western Indonesia. The families Typhlopidae (blind snakes) and Hydrophidae (sea snakes) and the aquatic colubrid genera *Hurria* and *Acrochordus* have been omitted from this report; nonetheless, they are represented in the Philippines.

Of the 69 genera of terrestrial snakes reported from Indonesia (many of which are of uncertain taxonomic status), 29 are known from the Philippines. Four genera[1] are endemic to the Philippines: *Myersophis, Oxyrhabdium, Cyclocorus,* and *Hologerrhum. Oxyrhabdium* is related to the genus *Xylophis,* a genus restricted to the Western Ghats in India. *Cyclocorus* and *Hologerrhum* are closely related to each other; they have no close relatives in southeastern Asia, Papua, or elsewhere, and may have originated in the Philippines from some early natricine ancestor.

Sixty-seven species of Philippine snakes (88 species and subspecies) are recognized in this paper. These may be divided into two general groups, those which are not endemic to the Philippines, and those which are restricted to the islands.

1. Non-endemic species. There are 32 non-endemic species represented in the Philippines either by subspecies found in Indonesia or by endemic subspecies related to populations which are found in Indonesia. Included among the non-endemic species are: *Ahaetulla prasina, Aplopeltura boa, Boiga angulata, Boiga cynodon, Boiga dendrophila, Boiga drapiezi, Calamaria everetti, Calamaria suluensis, Calamaria vermiformis, Chrysopelea*

1. After this paper had gone to press, a paper by Dr. Edward H. Taylor appeared in Copeia (1963, no. 2, pp. 429–433) in which he described a new genus and species of colubrid snake from Luzon Island, *Myersophis alpestris.* I have not seen the snake and do not feel qualified to comment upon this discovery at this time.

paradisi, Dendrelaphis caudolineatus, Dendrelaphis pictus, Dryocalamus subannulata, Dryocalamus tristrigatus, Dryophiops rubescens, Gonyosoma oxycephala, Liopeltis tricolor, Lycodon aulicus, Lycodon subcinctus, Maticora intestinalis, Naja naja, Natrix chrysarga, Ophiophagus hannah, Opisthotropis typica, Oligodon meyerinki, Oligodon vertebralis, Psammodynastes pulverulentus, Python reticulatus, Stegonotus mülleri, Trimeresurus wagleri, Xenopeltis unicolor, and *Zaocys carinatus.*

All of the species listed above are known to have western Indonesian-Malayan affinities. Many of the species are represented in the Philippines by distinct subspecies, as for example *Ahaetulla p. preocularis, Boiga d. divergens, Boiga d. latifasciata, Boiga d. multicincta, Calamaria v. grayi, Dendrelaphis c. luzonensis, Dendrelaphis c. terrificus, Maticora i. bilineata, Maticora i. philippina, Maticora i. suluensis, Naja n. philippina, Naja n. samarensis* and *Oligodon v. notospilus.*

In addition, a few species are also known from the Philippines which have been distinguished from closely related species listed above on the basis of a subjective evaluation of morphological differences. Several of these could be considered subspecies, as for example *Liopeltis philippina, Dryophiops philippina.* I regard these as good species, but differences in opinion regarding the taxonomic status of populations do exist among various workers. In any event, these species were derived from isolated populations of their Bornean relatives listed above among the non-endemic forms.

It must be noted that there are no species either of eastern Indonesian (Papuan) or Formosan origin in the Philippines.

II. Endemic species. There are thirty-four endemic species in the Philippines: *Boiga philippina, Calamaria bitorques, Calamaria gervaisi, Calamaria joloensis, Calamaria mearnsi, Calamaria zamboangensis, Calliophis calligaster, Cyclocorus lineatus, Elaphe erythrura, Hologerrhum philippinum, Liopeltis philippina, Lycodon dumerili, Lycodon Mülleri, Lycodon tessellatus, Myersophis alpestris, Natrix dendrophiops, Natrix auriculata, Natrix lineata, Natrix spilogaster, Oligodon ancorus, Oligodon maculatus, Oligodon modestus, Oligodon perkinsi, Opisthotropis alcalai, Oxyrhabdium leporinum, Oxyrhabdium modestum, Pseudorabdion ater, Pseudorabdion menamarae, Pseudorabdion montanum, Pseudorabdion oxycephalum, Pseudorabdion taylori, Sibynophis bivattatus, Trimeresurus flavomaculatus Trimeresurus schultzei,* and *Zaocys luzonensis.*

The relationships of each of the above-named species will be discussed in some detail in the series of systematic papers now in press. With the exception of the genera *Cyclocorus, Hologerrhum, Myersophis,* and *Oxyrhabdion,* and the species *Lycodon dumerili, L. mülleri, Oligodon perkinsi,* and *Trimeresurus schultzei,* all have relatives existing at the present time in Borneo.

Cyclocorus and *Hologerrhum* are probably congeneric, and most likely they have evolved in the Philippines from some natricine-like ancestor. *Lycodon dumerili* and *L. mülleri* are very closely related and are probably relics of an early, widely distributed lycodontine snake from which the highly specialized species of *Lycodon* were subsequently derived. The affinities of the Palawan species *Trimeresurus schultzei* and the Calamianes endemic *Oligodon perkinsi* are not known. The latter may have been derived from a "*purpurascens*-like" ancestor, while the former may be related to the "*popeorum*" section of the genus *Trimeresurus*. The genus *Oxyrhabdium* has no close relatives in the Indo-Malayan region. It is a very old genus related to the distant *Xylophis*, a genus of burrowing snakes restricted to Peninsular India.

It is very evident that, excepting the three genera *Cyclocorus*, *Hologerrhum*, and *Oxyrhabdium*, all the endemic species of Philippine snakes are related to western Indonesian species.

There are no endemic species in the Philippines which have eastern (Papuan) affinities, nor are there any genera or species having strictly Palearctic affinities.

FACTORS AFFECTING THE DISPERSAL OF PHILIPPINE SNAKES

Animals may have entered the Philippine Islands either by dispersal through a continuous and ecologically tolerable space, or by saltatory movements from one agreeable environment to another (Inger, 1954, p. 475). Insofar as the terrestrial snakes are concerned, it seems likely that the former has been most effective. Indeed, the very regular "immigrant pattern" of dispersal (Darlington, 1957, p. 485) of the Philippine snakes leads me to conclude that saltatory movements have had little effect on the fauna except for several of the smaller islands, not connected to any larger land mass (*e.g.*, Ticao, Sibuyan, Butan, Camiguin).

There are few problems in understanding the movements of animals through a continuous and ecologically agreeable environment, time to permit dispersal being the single most important factor. However, the mechanisms involved in the fortuitous dispersal of terrestrial snakes require a few words.

Because snakes move about with relative ease, lay eggs away from water, and can swim, it is frequently assumed that they can move with almost as much ease through a discontinuous environment as through a continuous biotope. We have very little data on the detailed ecological preferences of snakes beyond the obvious facts that some are obligate burrowers, some dwell on the ground and take refuge under logs or rocks or in holes at the bases of trees, others are arboreal or aquatic, and some appear to be

able to live in a variety of situations. Nevertheless, where groups of snakes have been studied with care, it has been shown that they show definite ecological preferences, as for example *Leptodeira*, an inhabitant of the moist tropical forests, and its close ally *Hypsiglena*, whose species live at higher elevations and in drier environments (Duellman, 1958, p. 126).

We have little knowledge of the ecological factors which limit the distribution of snakes in the Philippines. However, the uniformity of the lowland tropical environment in this region would suggest that those factors would have a minimum effect and wherever continuous land masses exist snakes would soon fan out through the entire area. On the other hand, in an archipelago-type of environment, terrestrial snakes would have to cross a sea barrier in order to move from one land mass to another, and this raises some distinct problems.

Snakes can swim, but this does not necessarily mean, *ipso facto*, that they can cross salt water barriers. Sea snakes, and the colubrid snakes of the genera *Hurria* and *Acrochordus*, all of which enter salt water, have several morphological adaptations which secure the animals against the vicissitudes of that hyperisotonic solution. Nasal valves are present which close off the nostril passages. The nostrils are located on the top of the head and permit breathing while the snake is in the water. The rostral cleft is almost absent and this prevents water from entering the mouth. And the skin is thickened, especially the interstitial skin between scales, and serves as a protection against loss of body fluids or penetration of the body by salt ions.

The terrestrial Philippine snakes lack all of the above modifications. Thus, any individual entering the sea would be exposed to its effects. Consequently, I strongly doubt that a terrestrial snake could live for long if it had to journey many miles in the sea in order to pass from one island to another.

Rafting certainly provides a satisfactory means for transporting snakes from one island to another, especially in the Malayan tropics. The entire Malayan area is one of heavy rainfall, and rain in large quantities frequently falls in short periods of time. Rivers rise rapidly and become very turbulent. Portions of their banks are often torn away, float downstream, and out to sea. These rafts are then carried about in the prevailing currents, which in the case of the Philippines move northward on both sides of the archipelago. Should chance permit, the raft may touch at some distant island, and any animals trapped when the bank was torn away presumably could avail themselves of the new locality. I believe that such an explanation may account for the present distribution of snakes on Batan and Camiguin islands, especially for the ground-dwelling snake *Trimeresurus flavomaculatus*. The three arboreal snakes also known from those islands may have arrived via other means (see below).

Typhoons, or high winds, are occasionally effective in moving animals

about. Inger (1954) has suggested that typhoons, which are not infrequent in the Philippines, probably have acted to disperse some elements of the amphibian fauna. Myers (1953, p. 21) has indicated that wind dispersal is available to smaller animals which may be carried aloft on pieces of vegetation, but that ground-dwelling animals probably would not be much affected. Three of the four species of snakes known from the remote Batan Island are light-weight arboreal snakes, and their presence on that island could possibly be the result of wind distribution. Dickerson (1928, fig. 6) has shown that an occasional typhoon tract will pass over northeastern Luzon, then veer almost due north, and pass over Batan and Camiguin islands.

Other factors which influence the distribution of terrestrial snakes include the size of the island, the width of the water barriers between islands, and man. Darlington (1957, p. 482) has discussed the effects of area as a limiting factor on the number of species which inhabit islands of different size. Unfortunately, the snake fauna of the islands of the Philippines has been unequally collected, the larger islands having attracted collectors more frequently than the smaller islands. Consequently, it is difficult at the present state of our knowledge of the distribution of Philippine snakes to be certain of the effects that island size has on the faunal composition.

In a like manner, it is not possible to evaluate the importance of distance between islands as a limiting factor in the distribution of Philippine snakes. As already mentioned, the regular distribution of snakes in the Philippines suggests that dispersal by saltatory movements, in which distance between islands would become a significant factor, probably has been of minor importance.

The effects that man has had on dispersing certain elements of the Philippine fauna can only be inferred. It is, of course, well known that certain reptiles are more likely than others to be transported about by man. The geckos of the genus *Gehyra* are prime examples. The present distribution of *Lycodon aulicus* may also be explained by allowing for a human agency in its dispersal. In the following discussion I have noted a few instances where man has probably been responsible for the occurrence of some snakes on certain islands.

On the whole, the Philippine snake fauna presents few problems to the zoogeographer. The distribution of these animals can be explained for the most part on the basis of former land connections for which geologic and hydrographic evidence provides a large measure of agreement.

ANALYSIS OF ISLAND FAUNA

In the following section the snake fauna of each of the Philippine islands from which terrestrial snakes have been reported and/or collected

is reviewed. The purpose of this review is to focus attention on the inter-island relationships of the snake fauna. Each island is briefly described as to its geographical position. Pertinent facts about the geology and hydrography are included. A brief discussion of the snake fauna known to inhabit the island, with comments on the probable routes of dispersal, then follows.

Balabac Island

Ahaetulla prasina prasina
Aplopeltura boa
Boiga dendrophila multicincta
Chrysopelea paradisi
Dendrelaphis caudolineatus caudolineatus
Dryocalamus tristrigatus
Elaphe erythrura philippina
Gonyosoma oxycephala
Maticora intestinalis bilineata
Natrix chrysarga
Oligodon vertebralis notospilus
Ophiophagus hannah
Psammodynastes pulverulentus
Trimeresurus schultzei
Trimeresurus wagleri
Xenopeltis unicolor

Balabac Island (07° 56.6′ N. Lat., 117° 01.0′ E. Long.) lies between North Borneo and Palawan Island. The island is fairly small, about 125 square miles in area.

There are no endemic species or subspecies of snakes on Balabac. All the species are also known from Borneo and Palawan. There are a number of snakes which have been reported from both Palawan and Borneo but which have not been taken on Balabac. These include *Boiga cynodon, B. drapiezi, Calamaria everetti, Dendrelaphis pictus, Liopeltis tricolor, Lycodon subcinctus, Naja naja, Python reticulatus, Sibynophis bivittatus* (or related Bornean species *S. geminatus*) and *Zaocys carinatus.* Some, if not all, of these species may be expected to occur on Balabac. Perhaps the larger snakes, *Python reticulatus, Naja naja,* and *Zaocys carinatus,* might not be found there because the small size of the island may act to limit the potential food supply.

Bantayan Island

Chrysopelea paradisi
Dendrelaphis caudolineatus terrificus
Lycodon aulicus capucinus

Bantayan Island (11° 13.0′ N. Lat., 123° 44.0′ E. Long.) lies at the north end of the Tañon Strait, to the northeast of Negros and northwest of Cebu. The island occupies an area of 45 square miles.

Bantayan rests upon the Visayan submarine shelf which lies at less than 50 meters depth and which joins Negros, Panay, Cebu, and Masbate islands.

Only three snakes have been collected on this island, all of which are widely distributed throughout the Philippines. The presence of *Dendrelaphis c. terrificus* relates this island to others lying south of Luzon on which a distinct subspecies of *D. caudolineatus* occurs.

Banton Island

Chrysopelea paradisi
Dendrelaphis caudolineatus terrificus

This small island (12° 56.5′ N. Lat., 122° 04.0′ E. Long.) of about 11 square miles in area lies in the Sibuyan Sea, about equidistant from Mindoro, Marinduque, and Tablas islands.

Only two species of snakes have been taken on the island. Both are widely distributed throughout the Philippines, *D. c. terrificus,* however, being found on the islands south of Luzon and Mindoro. Inasmuch as there is nothing known about the geological history of this island, and since hydrographic evidence does not suggest any reasonable chance of a subaerial land connection between this island and any of its neighbors, I suspect that the present fauna arrived via waif dispersal.

Basilan Island

Ahaetulla prasina preocularis
Aplopeltura boa
Boiga cynodon
Calamaria gervaisi hollandi
Calamaria vermiformis grayi
Chrysopelea paradisi
Cyclocorus lineatus nuchalis
Dendrelaphis caudolineatus terrificus
Lycodon dumerili
Natrix auriculata
Natrix dendrophiops dendrophiops
Natrix lineata
Oxyrhabdium modestum
Psammodynastes pulverulentus
Python reticulatus
Trimeresurus wagleri

Basilan Island is located immediately south of the Zamboanga Peninsula, Mindanao Island, between latitudes 6° 25′–6° 45.5′ N., and longitudes 121° 47.5′–122° 19.5′ E. The island occupies an area of about 495 square miles. There are many hills, but the most prominent is Basilan Peak, which reaches an altitude of 3320 feet. The narrow strait which separates Basilan from Zamboanga Province, Mindanao Island is a shallow submarine shelf, and it is very evident that Basilan must have been joined to Mindanao

during parts of the Pleistocene. In a like manner, Basilan must also have been joined to the islands of the Sulu Archipelago to its southwest which also lie on the same submarine platform, now at less than 50 meters depth.

There are no unique species of snakes on Basilan. Taylor (1928, p. 217) indicated that the caecilian *Ichthyophis monochrous* occurs on Basilan but not on Mindanao. Recently, however, Inger (1954, p. 207) reported *I. monochrous* from Mindanao. Based on the distribution of reptiles and amphibians, Basilan may best be regarded as part of Mindanao.

Batan Island

Ahaetulla prasina preocularis
Lycodon mülleri
Natrix spilogaster
Trimeresurus flavomaculatus mcgregori

Batan Island (20° 25.2′ N. Lat., 121° 57.7′ E. Long.) lies about 130 miles north of Luzon Island between Taiwan and Luzon. It is separated from Taiwan by the deep Bashi Channel and from the islands to the south by the Balintang Channel. Both of these channels are more than 6000 feet deep thereby precluding any reasonable chance for a subaerial land connection between it and either Taiwan or the southern islands. The island occupies an area of 27 square miles.

It seems likely that Batan Island was populated by snakes which arrived by fortuitous means, either by rafting, wind dispersal, or in the course of human activities. The former probably applies in the case of *Trimeresurus f. mcgregori,* a subspecies endemic to the island.

The other species, all arboreal, could also have arrived at Batan Island by rafting, the prevailing current patterns in the China Sea favoring movement from Luzon northward. Or, they could have been carried there by high winds (see p. 376). The specimens of these species which have been taken on Batan suggest that the Batan populations are taxonomically indistinguishable from the Luzon populations, and therefore have only recently become established there.

Bohol Island

Ahaetulla prasina preocularis
Dendrelaphis caudolineatus terrificus
Gonyosoma oxycephala
Naja naja samarensis
Natrix auriculata
Natrix lineata
Oxyrhabdium modestum
Psammodynastes pulverulentus
Python reticulatus
Trimeresurus flavomaculatus flavomaculatus

Bohol Island (09° 38.0′ N. Lat., 123° 52.5′ E. Long.) lies to the north of Mindanao from which island it is separated by the Mindanao Sea. The island occupies an area of 1492 square miles. The highest peaks are located near the center of the island and reach altitudes of almost 2600 feet.

The island lies on a high submarine ridge which joins it to Leyte. Bohol is separated from Cebu by the Bohol Strait, having depths in excess of 500 meters. Most of the island is capped by late tertiary limestone, except where stream erosion has stripped away the cover to reveal the basement complex of crystalline rocks. From this it is concluded that the island was uplifted since the late Tertiary, probably in Pleistocene times.

There are no endemic species or subspecies of snakes on Bohol. All forms are identical to those found on Mindanao, Samar, and Leyte islands. There are, however, a number of snakes, lizards, and amphibians which inhabit those latter islands but not Bohol. Unfortunately, our knowledge of the Bohol fauna is based upon a few, small, recent collections. The fauna is poorly known, and at the present time it is not possible to evaluate the significance of the absence of certain groups of reptiles and amphibians from those collections. It is reasonably certain, however, that the known Bohol fauna is most closely related to that from Mindanao, Samar, and Leyte. In spite of the proximity of Cebu Island, there is no evidence to indicate that there has been any faunal interchange between those islands.

Bongao Island

Elaphe erythrura philippina
Oligodon meyerinki
Psammodynastes pulverulentus
Xenopeltis unicolor

Bongao Island (05° 01.5′ N. Lat., 119° 45.1′ E. Long.) is a member of the Tawi-Tawi group in the Sulu Archipelago. It is the southernmost island in the Tawi-Tawi group and is separated from Tawi-Tawi and Sanga Sanga by the very narrow and shallow Bongao Channel. To the west, and separated by a channel about 32 miles wide, lies Borneo; the Sibutu islands lie about 20 miles to the south.

The entire Tawi-Tawi group of islands is on a high submarine shelf, extending from Zamboanga southward, which lies within 50 meters of the surface. This high shelf terminates at the southern end of Bongao Island where there is an abrupt drop to depths of about 300 meters in the Sibutu Passage. Although geological evidence is lacking, the faunal picture clearly indicates that a continuous submarine shelf must have extended from Mindanao to Borneo. The present deep Sibutu Passage was probably formed through block faulting sometime after mid-Pleistocene.

Three of the four species of snakes known from Bongao are also known

from North Borneo. *Elaphe e. philippina*, however, is known only from the Palawan Archipelago, and its occurrence on Bongao is unexpected. Unfortunately, I have not seen the specimens which were referred to that subspecies by Taylor (1922a, pp. 160–161). *Elaphe erythrura* has not been reported from Borneo. However, unless the Bongao specimens were introduced through human agencies, it seems very likely that the species will be found in Borneo.

Bubuan Island

Chrysopelea paradisi
Dendrelaphis caudolineatus terrificus
Liopeltis tricolor

This very small island (06° 20.9′ N. Lat., 121° 58.0′ E. Long.) is a member of the Tapiantana Group.

Only three species of snakes have been taken on this island. *Liopeltis tricolor* is well-known in Borneo and *Dendrelaphis c. terrificus* is widely distributed throughout the southern Philippines. *Chrysopelea paradisi* is widely distributed throughout the Malayan region.

The few snakes present on Bubuan relate this island to other members of the Sulu Archipelago, and thus, to Borneo and Mindanao. This is the northernmost locality for the Bornean *L. tricolor* in the eastern Philippines and the southernmost locality for *D. c. terrificus*.

Busuanga Island

Ahaetulla prasina prasina
Dendrelaphis caudolineatus caudolineatus
Dendrelaphis pictus pictus
Elaphe erythrura philippina
Liopeltis philippina
Maticora intestinalis bilineata
Natrix chrysarya
Oligodon vertebralis notospilus
Psammodynastes pulverulentus
Sibynophis bivittatus

Busuanga Island (12° 05.0′ N. Lat., 120° 05.0′ E. Long.), a member of the Calamianes Group, lies near the northern end of the Palawan submarine shelf. It is the largest island of the group, 344 square miles in area.

There are no endemic species of snakes on Busuanga; all are known from islands to the south, especially Palawan. A single remarkable genus and species of discoglossid frog, *Barbourula busuangensis*, is known only from this island and Palawan. This frog is the sole representative of the Palearctic frog family Discoglossidae to occur in the Oriental Region and

undoubtedly is a relic species which has been isolated on those islands for a long time.

Cagayan Sulu Island

Calamaria suluensis
Dendrelaphis pictus pictus

Cagayan Sulu (07° 01.0′ N. Lat., 118° 30.0′ E. Long.) is a small island, 26 square miles in area, which lies about 70 miles off the northeast coast of North Borneo. This island, together with its group of 13 surrounding islets, lies at the edge of the Bornean submarine shelf. The island is said to have several peaks, of which the highest is 837 feet and represents an extinct volcano (Smith, 1924, p. 244).

Only two snakes have been taken on Cagayan Sulu, both of which are known from Borneo.

Camiguin Island

Ahaetulla prasina preocularis
Chrysopelea paradisi
Dendrelaphis caudolineatus luzonensis
Trimeresurus flavomaculatus flavomaculatus

Camiguin Island (18° 55.7′ N. Lat., 121° 54.8′ E. Long.) belongs to the Babuyan Group and is located off the north coast of Luzon. The island is separated from Luzon by the Babuyan Channel, which is 100 to 500 meters deep. The highest peak on this island of 63 square miles is Camiguin Volcano which rises 2750 feet above sea level.

The snakes known from Camiguin are species and subspecies common on Luzon. *Dendrelaphis c. luzonensis,* however, is found only on Luzon and Camiguin.

There is no evidence to suggest how the snakes reached Camiguin. There may have been a land connection between it and Luzon, if the Babuyan Channel is of recent origin. If, on the other hand, the Babuyan Channel is an old structure, then rafting, wind dispersal, or accidental transport by human agencies could account for their presence on the island. In any event, the absence of geographic differentiation suggests the snakes have only recently become established there.

Catanduanes Island

Boiga angulata

This large island (13° 47.0′ N. Lat., 124° 16.0′ E. Long.) of 552 square miles area, lies off the southeast coast of Luzon. It lies on the broad, shallow Camarines shelf and undoubtedly has been joined to southeastern Luzon by subaerial land during parts of the Pleistocene.

A single snake has been taken on the island. The species is well known in the Philippines and has been reported from many of the larger islands, including Luzon, to which Catanduanes is obviously related by reason of its geographical and hydrographic position.

Cebu Island

Ahaetulla prasina preocularis
Calamaria gervaisi iridescens
Calliophis calligaster gemianulis
Chrysopelea paradisi
Cyclocorus lineatus lineatus
Dendrelaphis pictus pictus
Elaphe erythrura erythrura
Lycodon aulicus capucinus
Natrix dendrophiops negrosensis
Oxyrhabdium leporinum visayanum
Python reticulatus

This elongate island (10° 23.0′ N. Lat., 123° 53.3′ E. Long.), about 139 miles long and 20 miles wide, lies off the east coast of Negros Island, from which it is separated by the deep Tañon Strait. The mountains, which have a north-south trend, reach their greatest elevation in the central portion where Mt. Cabalasan attains an altitude of 3324 feet. Cebu lies on a very narrow shelf on its south, east and west sides, where there are abrupt drops to depths in excess of 500 meters. The northern portion of the island rests upon the shallow shelf which forms part of the broad, shallow submarine platform joining Cebu, Negros, Panay, and Masbate islands.

According to Dickerson (1928, p. 285) "Cebu was until late Pleistocene a string of coral islands which had but little connection with either the Visayan island to the west or the large Surigao island to the east."

There are no snakes unique to Cebu. Of the eleven species presently known from the island, seven are widely distributed throughout the Philippines. The four other species, *Calliophis c. gemianulis, Calamaria g. iridescens, Oxyrhabdium l. visayanum* and *Natrix d. negrosensis,* are identical to populations otherwise restricted to Negros and Panay. From this it seems reasonable to conclude that Cebu and Negros were joined together. The marked similarity of the fauna suggests that the islands were joined very recently, probably in the latest Pleistocene. Inasmuch as there are no endemic species of reptiles or amphibians on Cebu, it is doubtful that any of those animals were able to reach the island prior to that time. This would be in keeping with Dickerson's suggestion that Cebu was a series of small islands until late Pleistocene, and with McGregor's conclusion that Cebu probably was not joined to Negros during the Pliocene or most of the Pleistocene, based on the high degree of endemism among the birds.

CORON ISLAND

Ahaetulla prasina prasina
Dryophiops rubescens

Coron Island (11° 55.0′ N. Lat., 120° 14.0′ E. Long.) belongs to the Calamianes Group and lies to the immediate southeast of Busuanga. The island occupies an area of 27 square miles, is high and very rocky.

The two species of snakes reported from Coron are both well-known in Borneo. *Dryophiops rubescens* has not been taken on any other island in the Philippines, but it is reasonably certain that it will be found on Palawan unless it reached Coron by fortuitous means. *Ahaetulla p. prasina* has been taken on all the larger islands of the Palawan Archipelago, as well as Borneo.

CULION ISLAND

Ahaetulla prasina prasina
Boiga cynodon
Dendrelaphis pictus pictus
Elaphe erythrura philippina
Liopeltis philippina
Maticora intestinalis bilineata
Natrix chrysarga
Oligodon perkinsi
Sibynophis bivittatus

Culion Island (11° 50.0′ N. Lat., 119° 55.0′ E. Long.) is the second largest island in the Calamianes Group (150 square miles in area) and lies to the immediate south of Busuanga Island. Culion, Coron, and Busuanga form a compact group, the three islands being separated by narrow, shallow channels. From a zoogeographic standpoint the islands may be treated as a single unit.

Culion is, herpetologically, the best known of the Calamianes islands. Three species of snakes are known from Busuanga, two from Coron, and nine from Culion. Of the nine Culion species, *Oligodon perkinsi* appears to be endemic as is the frog genus *Barbourula* on Busuanga[2]. *Liopeltis philippina,* a species closely related to *L. tricolor* (known from western Indonesia and Palawan), has been taken on northern Palawan. I suspect that that species evolved in the Calamianes islands from an isolated population of *L. tricolor.* It probably entered Palawan during the last period of glacial maxima when the Palawan submarine shelf must have been exposed to subaerial erosion for its entire length. The remaining seven species and subspecies of Culion snakes are identical to those on Palawan.

Several fresh-water fish of the family Cyprinidae are found in the Calamianes islands. Four distinct species of cyprinid fish have been re-

2. Since this was written, specimens of *Barbourula* were taken on Palawan Island.

ported from Busuanga. Of these, one belongs to an endemic species of *Hampala,* and one to a distinct species, *Puntius ivis.* The two remaining species are found in Palawan.

Nine species of amphibians have been recorded from the Calamianes. Eight are known on Palawan. And one, *Rhacophorus a. appendiculatus,* reported from Culion on the basis of specimens obtained by Dr. Moellendorff, probably does not occur outside of the eastern Philippines (Inger, 1954, p. 376).

Cuyo Island

Lycodon aulicus capucinus

The largest of the Cuyo Islands, Cuyo (10° 51.1′ N. Lat., 121° 02.4′ E. Long.) lies about midway between northeastern Palawan and Panay islands. The island rests on the Palawan submarine shelf at the north end of the Sulu Sea. It is of volcanic origin with the highest point about 600 feet above sea level.

A single specimen of *Lycodon aulicus* has been collected on this isolated island. I suspect it was introduced there by man.

Dinagat Island

Oxyrhabdium modestum
Psammodynastes pulverulentus

Dinagat Island (10° 05.0′ N. Lat., 125° 35.0′ E. Long.) lies to the immediate north of the Surigao Peninsula, Mindanao. On the west, the Surigao Strait separates Dinagat and Leyte, and on the north, the Leyte Gulf separates the island from Samar. Mindanao and Dinagat are separated by a shallow channel five miles in width. The island occupies an area of 309 square miles. A chain of mountains extends from north to south. There are several peaks attaining altitudes in excess of 1700 feet; the highest point is at the north end of the island and rises 3300 feet above sea level.

Dinagat, Samar, and Leyte islands are joined to Mindanao by a shallow submarine shelf. This shelf lies well within 50 meters of the surface and undoubtedly was exposed to subaerial erosion at times of glacial maxima during the Pleistocene. At those times these islands and Bohol, which is connected to Leyte by a similar shallow submarine shelf, must have formed a continuous land mass, and there must have been relatively free movement of faunal elements from one island to another.

Two snakes have been reported from Dinagat. *Psammodynastes pulverulentus* is widely distributed throughout southeastern Asia. *Oxyrhabdium modestum* is known from Mindanao, Samar, Leyte, and Bohol (also doubtfully recorded from Negros).

Seven of the eight species of frogs Inger (1954, p. 512) records from

Dinagat are also found on Mindanao, Samar, and Leyte. Of these, three are restricted to those islands and four are widely distributed throughout the Philippines. Only one, *Rana macrodon visayanum*, known from the western Visayan islands but not from Mindanao or Samar, presents difficulties. Inger states that that frog occurs on Leyte as well as Dinagat. It is interesting to note that of the 16 frogs known from Leyte, this is the only frog not known to occur on Mindanao. Although Inger does not discuss this interesting anomaly, I believe it is reasonable to assume that *Rana m. visayanum* is not native to either Leyte or Dinagat. Taylor (1923, p. 523) has indicated that *Rana macrodon* is frequently sought after by the native inhabitants in the western Visayan islands as a source of food. I suspect that this frog may have been introduced into Leyte and Dinagat either accidentally or as a potential food source.

Jolo Island

Ahaetulla prasina preocularis
Calamaria joloensis
Chrysopelea paradisi
Dendrelaphis pictus pictus
Elaphe erythrura erythrura
Maticora intestinalis suluensis
Oligodon meyerinki
Ophiophagus hannah
Psammodynastes pulverulentus
Python reticulatus
Trimeresurus flavomaculatus flavomaculatus
Trimeresurus wagleri
Xenopeltis unicolor

The largest of the Sulu Islands, Jolo (06° 00.0′ N. Lat., 121° 09.0′ E. Long.) lies about midway between Basilan on the northeast and Tawi-Tawi on the southwest. Between Jolo, Basilan, and Tawi-Tawi are many small islands, some of volcanic origin and some merely raised coral reefs. Taken together, these islands represent the high points on the Sulu submarine platform, which extends from Zamboanga to Tawi-Tawi. According to Smith (1924, pp. 247–248) this platform has successively submerged and emerged, producing alternately a discontinuous and a continuous land mass extending from Mindanao to Borneo.

Jolo Island has an area of 345 square miles. There are several peaks, the highest of which, Mt. Bud Dajo, rises 2894 feet above sea level. The island is of volcanic origin. No active volcanoes are now present on the island, but there are extensive deposits of volcanic ash and tuffs presumed to be of late Pliocene and Pleistocene age.

The snake fauna of Jolo includes elements of the Mindanao and Bornean faunas. *Oligodon meyerinki*, related to the Bornean *O. octolineatus*, and

Xenopeltis unicolor are typical modern Bornean elements, while *Aheatulla p. preocularis, Elaphe e. erythrura,* and *Trimeresurus f. flavomaculatus* represent the typical Mindanao elements. Two species are thought to be endemic to Jolo, *Calamaria joloensis* and *Maticora i. suluensis.* The latter is very close to the Bornean *M. i. nigrotaeniata,* but the former does not appear to have any close relatives, either in Borneo or in the Philippines.

From the above it would seem that the island has been subject to several faunal invasions. The earliest, probably in late Pliocene or early Pleistocene, allowed the progenitors of the modern Mindanao-eastern Philippine fauna to enter those islands. During the later Pleistocene, modern elements of the Bornean fauna have passed northward toward Mindanao, and at the same time elements of the Mindanao fauna have moved southward.

The systematics of the Bornean species of *Calamaria* is too poorly known to permit speculation regarding the status of *C. joloensis.* At present, it appears to be a very distinct species and may represent either a relic form of an old invasion or a recently evolved unique species. On the other hand, a closely related but unknown species may yet be discovered in Borneo.

Kalotkot Island

Chrysopelea paradisi
Dendrelaphis caudolineatus terrificus

This small island (14° 54.5′ N. Lat., 122° 08.8′ E. Long.) lies off the east coast of Polillo Island. According to Taylor (1922b, p. 162) the island is about "3 kilometers long and is heavily forested."

Taylor states that he obtained three species of snakes on Kalotkot and eleven species of lizards. I have been able to establish the identity of only two of the snakes he obtained there and find they are identical to species found on Polillo. One very interesting fact is that *Dendrelaphis c. terrificus,* which occurs on Kalotkot and on Polillo, is not found on Luzon Island, but rather appears to be restricted to the islands of the southern and central Philippines. This interesting case of discontinuous distribution is discussed more fully under Polillo Island (p. 402).

Lapac Island

Dendrelaphis pictus pictus

Lapac (05° 32.0′ N. Lat., 120° 46.2′ E. Long.) is a small island, about 16 square miles in area, belonging to the Tapul Group in the Sulu Archipelago. The island is covered by deeply weathered volcanics (Smith, 1924, p. 247) including a basalt flow overlying a volcanic tuff (Corby, 1951, p. 308).

A single arboreal snake has been taken here. The species is widely distributed throughout the Philippines and western Indonesia.

Leyte Island

Ahaetulla prasina preocularis
Boiga angulata
Boiga cynodon
Calamaria vermiformis grayi
Chrysopelea paradisi
Dendrelaphis caudolineatus terrificus
Elaphe erythrura erythrura
Naja naja samarensis
Natrix auriculata
Oxyrhabdium modestum
Psammodynastes pulverulentus
Python reticulatus
Stegonotus mülleri
Trimeresurus flavomaculatus flavomaculatus
Trimeresurus wagleri
Zaocys luzonensis

Leyte (10° 50.0′ N. Lat., 124° 52.0′ E. Long.) is the eighth largest island in the Philippines and occupies more than 2780 square miles. The island lies between Luzon and Mindanao; it is almost in contact with Samar Island along the latter's southwest coast but is separated by a very narrow and shallow channel of water. The island is very mountainous, many of the peaks representing extinct volcanoes. Tertiary and later volcanics overlie much of the central portion of the island and limestones, marls, and shales, some of late Tertiary age, cover much of the southern portion. There is every reason to believe that the northern parts of Leyte have been exposed for most, if not all, of late Tertiary and recent times and that until recently, Samar and Leyte were joined by continuous dry land.

The fauna of Leyte is very similar to that on Samar and Mindanao. A number of species, including *Calamaria v. grayi, Naja n. samarensis, N. auriculata, O. modestum,* and *Stegonotus mülleri* are known only from those islands within the Philippines. *Zaocys luzonensis,* a species otherwise found only on Luzon and Polillo, was reported from Leyte by Boettger (1890, p. lxiii). However, this needs confirmation.

Inger (1954, p. 512) records 16 species of frogs from Leyte. Of these, twelve are also found on Mindanao, three are suspect of being endemic to the island, and one has been reported from Luzon and Polillo but not elsewhere. The latter record is for *Rana signata similis* of which Inger examined six specimens said to have come from Cabalian, Leyte (Inger, 1954, p. 323). I doubt that that subspecies of *Rana signata* is indigenous to Leyte and suspect that, barring accidental mislabeling of the specimens, the frogs were accidentally introduced into the island.

Data drawn from the distribution of other groups of animals clearly

support the conclusions stated above regarding the faunal relations of Leyte, Samar, and Mindanao.

Lubang Island

Gonyosoma oxycephala
Natrix spilogaster

Lubang Island (13° 46.5′ N. Lat., 120° 11.5′ E. Long.) lies off the southwest coast of central Luzon opposite Batangas Province. It is separated from both Luzon and its southern neighbor, Mindoro, by deep channels. According to Smith (1924, pp. 258–260) the island is composed principally of igneous and metamorphosed sedimentary rocks with some coralline deposits along the coasts.

One of the two snakes reported from Lubang Island (*Gonyosoma oxycephala*) is widely distributed throughout southeast Asia. *Natrix spilogaster*, however, is found only on Luzon and Lubang islands. Inger (1954, p. 512) records two amphibians from the island, but again both are widely distributed forms. McGregor (1928, p. 205) suggests that Lubang Island belongs to the Luzon faunal province, based on the distribution of birds. On the other hand, Cooke, quoted in Dickerson (1928, pp. 269, 271, figs. 60, 61) indicates in his maps that Lubang properly belongs to a distinct Mindoro province. Insofar as snakes are concerned, Lubang, Mindoro, and Luzon should be combined into a single faunal district (see discussion of Mindoro, p. 394). The absence of numbers of amphibians and reptiles suggests that the present fauna on Lubang has probably been derived through fortuitous circumstances (rafting or accidental transport by man).

Luzon Island

Ahaetulla prasina preocularis
Boiga angulata
Boiga cynodon
Boiga dendrophila divergens
Boiga philippina
Calamaria bitorques
Calamaria gervaisi gervaisi
Calliophis calligaster calligaster
Chrysopelea paradisi
Cyclocorus lineatus lineatus
Dendrelaphis caudolineatus luzonensis
Dendrelaphis pictus pictus
Dryophiops philippina
Elaphe erythrura erythrura
Gonyosoma oxycephala
Hologerrhum philippinum
Lycodon aulicus capucinus

Lycodon mülleri
Lycodon tesselatus
Maticora intestinalis philippinus
Myersophis alpestris (see footnote 1, p. 373)
Naja naja philippinensis
Natrix dendrophiops barbouri
Natrix spilogaster
Oligodon ancorus
Oligodon modestum
Ophiophagus hannah
Oxyrhabdium leporinum leporinum
Psammodynastes pulverulentus
Pseudorabdion mcnamarae
Python reticulatus
Trimeresurus flavomaculatus flavomaculatus
Trimeresurus wagleri
Zaocys luzonensis

Luzon (15° 00.0′ N. Lat., 121° 00.0′ E. Long.) is the largest island in the Philippine Archipelago, with an area of 40,420 square miles. It is characterized by great irregularity and diversity of form. The northern portion of the island is dominated by a central Cordillera and the western Zambales Mountains. A broad plain extends from the Tayabas Isthmus north to Manila Bay. It narrows in passing between the Zambales Mountains and the central Cordillera and extends northward to the Lingayan Gulf. A number of volcanoes (some recently active) dominate the landscape: Mt. Marivales, Mt. Arayat, Mt. Makiling, Mt. Taal, and others. To the south of the Tayabas Isthmus are the Bondoc and Camarines peninsulas, the former composed of folded sedimentary rocks, the latter studded with volcanoes (Iriga, Isarog, Mayon, *et al.*) except in the north where there are folded sedimentary rocks.

Dickerson (1928, pp. 92–96) has shown that in all probability the island was divided into at least three smaller islands during the Pleistocene: (1) the Zambales highlands, (2) most of northern Luzon and perhaps incorporating Polillo Island, and (3) the Camarines Peninsula, which was joined to Samar. The Manila Plain was inundated part of that time.

Thirty-four species and subspecies of snakes are known to occur on Luzon Island. Of this number, three species, *Boiga philippina, Calamaria bitorques,* and *Lycodon tessellatus,* all of questionable status, are confined to the island. *Natrix spilogaster,* also known from Lubang Island off the western Luzon coast, is otherwise confined to Luzon. Several other species are confined to Luzon and its immediate neighbors, *i.e.,* Mindoro, Polillo, the Batanes islands. These include *Boiga d. divergens, Calamaria g. gervaisi, Calliophis c. calligaster, Dendrelaphis c. luzonensis, Hologerrhum philippinum, Lycodon mülleri, Myersophis alpestris, Naja n. philippinus, Natrix*

d. barbouri, Oligodon ancorus, and *Oxyrhabdium l. leporinum.* The remaining eighteen species and subspecies are widely distributed throughout the Philippines with the exception of *Cyclorus l. lineatus,* known elsewhere only from the Visayan Islands.

All endemic Luzon species, excepting those of the genera *Myersophis, Oxyrhabdium,* and *Cyclocorus,* are related to genera and species presently living in Indonesia. *Oxyrhabdium* apparently represents a very old group. Its closest relative, the genus *Xylophis,* is confined to the Western Ghats, in India. The genus *Cyclocorus* has no close relatives outside of the Philippines. A single widely distributed species is recognized within the islands, and I suspect that the genus had its origin in the Philippines.

Inger (1954, p. 513) recognizes twenty-two frogs from Luzon. Nine species and subspecies are either endemic to Luzon or are restricted to Luzon and its immediate neighbors. There are no unique genera of frogs on Luzon.

There is close agreement in the distributional picture of Luzon snakes and frogs and of the birds, insects, and land molluses.

Masbate Island

Lycodon aulicus capucinus
Natrix dendrophiops negrosensis

Masbate (12° 15.0′ N. Lat., 123° 30.0′ E. Long.) is a moderate-sized island, 1571 square miles in area, located near the southwestern coast of southern Luzon and northwestern Samar. It is separated from those islands by the deep Ticao and Samar straits. To the southwest of Masbate is the shallow Visayan Sea which now separates Masbate from Panay, Negros, and northern Cebu. The highlands on Masbate extend from southeast to northwest along the northeastern coast. There are several mountains which attain elevations of about 2000 feet.

Masbate rests upon the shallow Visayan submarine shelf. The faunal evidence (see below) suggests that Masbate has been associated with Negros and Panay during the recent past.

Only two snakes have been collected on Masbate. Of these, *Natrix d. negrosensis* is a subspecies found only on Panay, Negros, and Cebu.

Inger (1954) does not list any amphibians from this island but I have seen some material not available to him at the time his report was prepared. The affinities of the frogs from Masbate seem to lie with the Negros populations. McGregor (1928, p. 202) suggests that Masbate is allied to Negros on the basis of its avian fauna, although there are about half as many species known from the islands are are known from Negros. In a like manner, Schultze (1928, p. 253, fig. 58 and p. 254) includes Masbate in the Visayan faunal district on the basis of similarities in Lepidoptera fauna, and Cooke (1892) indicates a similar relation for the land molluses.

MINDANAO ISLAND

Ahaetulla prasina preocularis
Aplopeltura boa
Boiga angulata
Boiga cynodon
Boiga dendrophila latifasciata
Calamaria gervaisi hollandi
Calamaria mearnsi
Calamaria vermiformis grayi
Calamaria zamboangensis
Chrysopelea paradisi
Cyclocorus lineatus nuchalis
Dendrelaphis caudolineatus terrificus
Dendrelaphis pictus pictus
Elaphe erythrura erythrura
Lycodon aulicus capucinus
Lycodon dumerili
Maticora intestinalis philippina
Naja naja samarensis
Natrix auriculata
Natrix dendrophiops dendrophiops
Natrix lineata
Oligodon maculatus
Oligodon modestum
Oligodon vertebralis notospilus (?)
Ophiophagus hannah
Opisthotropis alcalai
Oxyrhabdium modestum
Psammodynastes pulverulentus
Pseudorabdion ater
Pseudorabdion taylori
Python reticulatus
Stegonotus mülleri
Trimeresurus flavomaculatus flavomaculatus
Trimeresurus wagleri

Mindanao (08° 00.0′ N. Lat., 125° 00.0′ E. Long.) is the second largest island in the Philippine Archipelago, occupying an area of more than 36,500 square miles. There are several mountain ranges and broad, flat stream valleys. Dickerson (1928, pp. 85–87) presents a summary of the Pleistocene history of Mindanao in which he demonstrates that Mindanao was divided into five islands in early Pleistocene. He (Dickerson, 1928, pp. 80–81) suggests that only the extreme eastern and extreme southwestern parts of Mindanao were uplifted during Miocene times. In the Pliocene, Dickerson (1928, p. 85) further suggests that western Mindanao was joined with Borneo via a Sulu bridge. Smith (1924, p. 218), in his concluding remarks, states that for the most part Mindanao is a young island, and "The great extent of comparatively recent volcanic extrusives and the considerable development of raised Pleistocene reefs gives one the impression that the

dominant processes in Mindanao have been aggradational rather than degradational."

The snake fauna of Mindanao is composed of at least two Bornean elements and a small Luzon element. An older group of endemics, a few of which are also found on Samar, Leyte, and Bohol, include *Calamaria mearnsi, Lycodon dumerili, Natrix auriculata, Natrix d. dendrophiops, Oligodon maculatus, Pseudorabdion taylori,* and *Stegonotus mülleri.* The latter is a relic species found also in North Borneo. Neither *Calamaria mearnsi, Lycodon dumerili, Natrix dendrophiops,* nor *Natrix auriculata* appears to have close relatives in Borneo at the present time. *Oligodon maculatus* is a very distinctive species; it was probably derived from an isolated population of *O. purpurascens,* as was the Luzon species *O. ancorus.* Lastly, *Pseudorabdion taylori* appears to be allied to the Bornean species of *Pseudorabdion* formerly assigned to the genus *Agrophis* (Leviton and Brown, 1959). It seems likely that the species noted above evolved from ancestral Bornean populations which entered Mindanao during the Pliocene.

A second group of species and subspecies, also restricted to Mindanao, Samar, Leyte, and Bohol, of more recent origin and closely allied to populations now living in Borneo, includes *Ahaetulla p. preocularis, Boiga d. latifasciata, Calamaria v. grayi, Calamaria zamboangensis, Dendrelaphis c. terrificus, Maticora i. philippina, Naja n. samarensis,* and *Oligodon v. notospilus.* These probably are derivatives of Bornean populations which entered Mindanao during the Pleistocene by way of a subaerial land bridge that must have extended from Borneo, via the Sulu Archipelago, to the Zamboanga Peninsula. (See also Herre [1928] and Myers [1951] who have provided abundant evidence to indicate that Borneo and Mindanao were joined by subaerial land sometime in the Pleistocene in order to account for the present distribution of obligate fresh-water fish on Mindanao; I am in full accord with those authors, based on the distribution of the snakes.)

A few subspecies of snakes, related to populations on Luzon, are also recorded from Mindanao. These include *Calamaria g. hollandi, Cyclocorus l. nuchalis,* and *Trimeresurus f. flavomaculatus.* The latter form, although placed in the same taxonomic category as the Luzon population, differs slightly, suggesting incipient subspeciation. I suspect that *Cyclocorus l. nuchalis* was derived through insular isolation from *C. l. lineatus.* The latter probably entered Mindanao when the Camarines Peninsula was joined to Samar and Mindanao sometime during the Pleistocene. The differences between *Calamaria g. hollandi* and *C. g. gervaisi* suggest that they evolved independently from isolated populations of a common ancestor.

Mindoro Island

Calamaria gervaisi gervaisi
Calliophis calligaster calligaster

Chrysopelea paradisi
Cyclocorus lineatus lineatus
Dendrelaphis caudolineatus luzonensis
Dendrelaphis pictus pictus
Dryophiops philippina
Elaphe erythrura erythrura
Lycodon aulicus capucinus
Lycodon mülleri
Naja naja philippinensis
Natrix dendrophiops barbouri
Oligodon ancorus
Ophiophagus hannah
Python reticulatus
Trimeresurus flavomaculatus flavomaculatus

This island (12° 50.0′ N. Lat., 121° 10.0′ E. Long.) lies to the southwest of Luzon Island. There are approximately 3759 square miles of land, excluding immediately adjacent islands (*e.g.*, Ilin, Ambulong, Buyallao, *et al.*), which together constitute Mindoro Province. The island is divided by a north-south trend of mountains, of which Mt. Halcon (8481 feet) in the north and Mt. Baco (8160 feet) in the center are the most prominent.

The island is separated from Luzon by the block-faulted Verde trough on the north, from the Palawan Archipelago by the Mindoro Strait on the southwest, and from other southern and eastern islands by the Tablas Strait.

The central and northwestern portions of Mindoro are composed of basement complex rocks, including andesites, granites, diorites, and other coarsely crystalline igneous rocks and some metamorphic rocks such as schists and slates. At the southern end are several limestones of mid- to late-Tertiary age (? Miocene and Pliocene) and some earlier limestones presumed to be of Mesozoic age because of the presence of fossil ammonites. The southwest coast is covered by a recent alluvium which evidently overlies late Tertiary limestones. Alluvium also covers much of the eastern coastal region. A small Mesozoic outcrop has been identified in the vicinity of Mt. Dumali, and a little late Tertiary limestone has been found in the vicinity of Varadero Bay. It is noteworthy that Verde Island and the immediately opposing shore of Luzon Island are covered by similar sediments and by extensive deposits of volcanic tuffs of relatively recent age.

Sixteen species and subspecies of terrestrial snakes are known from Mindoro. Not one is endemic to that island; all are known from Luzon. Six species and subspecies are endemic to Luzon and Mindoro and three to those islands and to Polillo and Batan. The seven remaining species are widely distributed throughout the Philippines and western Indonesia.

There are no species or genera of snakes common to Mindoro and the islands of the Palawan Archipelago which are not found in the eastern Philippines. This is likewise true for the amphibians (Inger, 1954, pp. 513–

514) and for insects (Schultze, 1928), but not for birds or primary fresh-water fish. According to Ripley and Rabor (1958, pp. 11–12) at least five species and subspecies of birds are common to Mindoro and Palawan and are not known from elsewhere. Herre (1928, p. 244) suggests that the single endemic cyprinid fish found on Mindoro, *Puntius hemictenus*, entered that island from Palawan. A distinctive species of timarau, *Bubalus mindorensis*, is known from Mindoro but not elsewhere in the Philippines. It is related to another species of *Bubalus* found in Sarawak, Borneo.

On the whole, the present fauna of Mindoro seems to be related to that on Luzon (although McGregor [1928] suggests otherwise based on bird distribution [see below]). The presence of a unique endemic species of *Bubalus* points to an early subaerial land connection between Mindoro and the Palawan islands. When this connection existed is in doubt. Dickerson (1928, p. 91) suggests that the Mindoro *Bubalus* was derived from an early Pleistocene or Pliocene ancestor, implying a possible land connection at that time.

The marked similarity in fauna between Mindoro and Luzon points to a relatively recent connection between those two islands, possibly in the late Pleistocene. As I have already indicated, the populations of snakes and frogs on Mindoro are taxonomically indistinguishable from those on Luzon. It is true that several genera of snakes known from Luzon, *e.g.*, *Zaocys*, have not been taken on Mindoro. However, the latter island is very poorly known, and consequently negative evidence of this sort is of little significance.

The unique species of fresh-water fish, *Puntius hemictenus*, known from Mindoro, is related to species found on Palawan Island. No indigenous species of fresh-water fish is known from Luzon. Two fresh-water fishes have been recorded from central Luzon. One, *Oryzias luzonensis* (Herre) belongs to a secondary group of fresh-water fishes, according to Myers (1951). The other, a loach of the genus *Cobitus* appears to be a Chinese species. Professor Myers suggests (*in litt.*) that the latter may have been introduced. These facts have been interpreted to mean that Luzon and Mindoro have been disconnected for a longer period of time than Palawan and Mindoro. Evidence from other groups of animals does not bear this out. Therefore, I offer below an alternative explanation to account for the presence of a species of fresh-water fish on Mindoro but not on Luzon in the belief that Mindoro and Luzon were joined by a subaerial land-bridge more recently than Palawan and Mindoro.

If it be assumed that the fresh-water fish *P. hemictenus* was present on Mindoro at the time that Mindoro and Luzon were joined by dry land, then it could be expected that the fish might have reached Luzon. Luzon and Mindoro could only have been joined across the Verdes Island Passage which now separates northern and northeastern Mindoro and the Batangas-Cavite districts of southwestern Luzon. If, at the time Mindoro and Luzon were joined together, the Mindoro population of *Puntius* were to disperse into

Luzon, the fish would have had to enter the streams which drain the Batangas-Cavite area. The Batangas-Cavite district is overlain by thick deposits of volcanic tuff derived from intermittent periods of volcanic activity in that district during the late Pliocene and Pleistocene. It is evident that there must have been periodic destruction of the existing habitats, including the streams. There must have been considerable destruction of life, also. The chances for a small population of fresh-water fish to become established in this area of Luzon would be very small, if not nonexistent. The above factors probably would have had little effect on the dispersal of the numerically larger populations of animals on Luzon into Mindoro, however. Even if the Batangas-Cavite region were temporarily denuded of life because of volcanic activity, dispersal of faunal elements from immediately adjacent parts of Luzon into that region would continue during tranquil periods as soon as the necessary habitats reappeared. Thus, movements of animals from Luzon into Mindoro could also continue, albeit on an interrupted basis. From the above, then, it follows that periodic destruction of the available habitats of *Puntius* in the Batangas-Cavite district probably acted as the limiting factor in preventing the establishment of permanent population of that fish on Luzon.

One further point may be noted. Palawan may have received its complement of fresh-water fish during the Pleistocene when the Sundaland submarine shelf was exposed to subaerial erosion. At that time fresh-water fish probably passed from the Malay Peninsula into the islands of western Indonesia. In 1941, Dickerson discussed the effects of the last glaciation (Wisconsin) on the Sundaland shelf. He indicated that the Moelengraaf river and valley existed "in varying forms . . . during the earlier glacial phases of the Pleistocene." (Dickerson, 1941, p. 14.) From this it may be assumed that the fresh-water fish now found on Palawan, and which are represented by a number of endemic species, may have entered that island in early or mid-Pleistocene. At least one species of fish was then able to reach Mindoro, also in early or mid-Pleistocene. This latter conclusion is based on the fact that Mindoro lacks all the modern species of snakes and amphibians, except those which are widely distributed throughout the eastern Philippines, and I find it difficult to believe that one group of animals could have entered Mindoro to the exclusion of all other groups. Thus, it is assumed here that the progenitor of *Puntius hemictenus* entered Mindoro about the same time as the ancestors of the unique timarau.

As I have noted above, McGregor (1928) believes that Mindoro is very distinct from Luzon. This conclusion is, in large part, based on the absence of the large hornbills, or calaos, from Mindoro. I do not believe that McGregor's conclusions are entirely justified, however. I have already pointed out above that any faunal movements from Luzon to Mindoro would have had to pass through the Batangas-Cavite corridor. Periodic volcanic activity closed this route. Time would be required to re-establish favorable habitats

for animals to reinhabit. In the case of the hornbills, they would have had to await the regrowth of the heavy dipterocarp forest climax. On the other hand, among the first animals to reinvade the Batangas-Cavite district would be the reptiles, many of which have wide ranges of ecological tolerances. These, then, would be the animals which could take advantage of a geologically temporary land connection between Luzon and Mindoro. In Dammerman's (1948) study of the fauna of Krakatoa, he showed that reptiles were among the earliest colonizers of that island following the 1883 explosion. On page 296, Dammerman also notes that ground snakes were the earliest colonizers of the slopes and surrounding areas of Mt. Jorullo, Mexico, which erupted in 1759. It is interesting to note that there are 12 species of ground snakes on Mindoro, and only two species of arboreal snakes. Most of the genera of arboreal snakes known from Luzon are absent, thus suggesting that the Batangas-Cavite corridor was not heavily forested at any time during which Mindoro and Luzon were joined together.

Negros Island

Ahaetulla prasina preocularis
Boiga angulata
Calamaria gervaisi iridescens
Calliophis calligaster gemianulis
Chrysopelea paradisi
Cyclocorus lineatus lineatus
Dendrelaphis caudolineatus terrificus
Dendrelaphis pictus pictus
Dryophiops philippina
Elaphe erythrura erythrura
Gonyosoma oxycephala
Lycodon aulicus capucinus
Natrix dendrophiops negrosensis
Oligodon modestum
Ophiophagus hannah
Oxyrhabdium leporinum visayanum
Oxyrhabdium modestum[3]
Psammodynastes pulverulentus
Pseudorabdion mcnamarae
Pseudorabdion montanum
Pseudorabdion oxycephalum
Python reticulatus
Trimeresurus flavomaculatus flavomaculatus
Trimeresurus wagleri

3. A single specimen of this snake was presented to Dr. Walter Brown, in 1954, by a resident of Dumaguete, Negros Oriental, who stated he had collected the specimen in the vicinity of the town. This species is well known in the eastern Philippines. Although Dr. Brown and Mr. Angel Alcala have collected in the southern Negros area extensively on and off during the last eight years, no other specimen of this species has been found on the island. If the species now occurs there, which is doubtful, it must certainly have been accidentally introduced within recent years.

Negros Island (10° 00.0′ N. Lat., 123° 00.0′ E. Long.) is the fourth largest island in the Philippine Archipelago, occupying an area of more than 4900 square miles. The island lies to the northwest of Mindanao and is in close proximity to Panay and Cebu. It is bounded on the north by the shallow Visayan shelf which joins it to Panay, Masbate, and the extreme northwestern coast of Cebu.

Northern and southern Negros appear to have been subject to extensive volcanic activity. The landscape of both regions is dominated by volcanoes; in the north Mt. Canlaon rises to 8087 feet; in the south Cuernos de Negros attains an altitude of 6244 feet. Between the northern and southern districts is a central region in which extensive sedimentary deposits are most prominent. Limestones of Pliocene age have been found near the summits of the eastern mountains. The western shores of Negros have been built up partly by sediments derived from the eastern mountains and partly by the outpouring of lava, ash, and boulders, beginning in late Pliocene and continuing into recent times. During the Pliocene, and perhaps part of the Pleistocene, Negros Island was divided into two parts, separated by a submerged central region. The present island is, therefore, of comparatively recent origin.

During the Pleistocene, at least the northern portion of Negros must have been joined to Panay and Masbate by a subaerial land bridge when the shallow Visayan shelf was exposed. Northern Cebu must also have been a member of this complex, as I have already explained (see discussion of Cebu, p. 384).

The snake fauna of Negros includes at least seven species and subspecies of which one is endemic (*Pseudorabdion montanum*) to Negros and six are known only from the Visayan complex. The other seventeen species are widely distributed throughout the archipelago.

Of the six species and subspecies endemic to the western Visayan Island, all have their closest allies on Luzon. *Calamaria g. iridescens* is very close to *C. g. gervaisi; Calliophis c. gemianulis* and *C. c. calligaster* are found only on the Visayan Islands and Luzon, with a third subspecies restricted to Polillo; *Natrix d. negrosensis* is more similar to *N. d. barbouri* from Luzon than to *N. d. dendrophiops*, the Mindanao subspecies; *Oxyrhabdium l. visayanum*, found only in the western Visayan Islands, is related to *O. l. leporinum* from Luzon; and *Pseudorabdion mcnamarae* is most closely allied to *P. minutum* from Luzon (which has been tentatively referred to the synonymy of the former).

The Negros fauna, or more properly the western Visayan snake fauna, was derived largely from Luzon. Only one member of the southern Philippine snake fauna, not also found on Luzon, is present on Negros, *Dendrelaphis c. terrificus* (the occurrence of *Oxyrhabdium modestum* on Negros has already been questioned [see p. 398]).

On the whole, the frogs have a pattern of distribution similar to that of

the snakes. A distinct subspecies of *Kaloula conjuncta,* most closely allied to the Luzon subspecies, occurs on Negros, and *Cornufer hazelae* appears to be restricted to Negros, Panay, and Luzon. A few frogs are allied to eastern or southern populations rather than the Luzon populations. Inger (1954, pp. 470–471) indicates that Negros shows about the same degree of faunal similarity to Mindanao as it does to Luzon and is, therefore, intermediate between the two.

Of the six subspecies of snakes endemic to the western Visayans which have their closest allies in Luzon, five are burrowing or at least secretive snakes. In view of the fact they are represented by distinct subspecies, it does not seem possible that their present distribution could be accounted for by recent accidental introduction by man, nor does it seem likely that the progenitors of so large a number of forms could have arrived by fortuitous rafting, or wind transport (which, incidentally, would be unlikely because prevailing storm paths do not pass from Luzon to the western Visayans). Furthermore, it is highly improbable that the ancestors of the Visayan species traveled across open water, for reasons I have already outlined (p. 376). Consequently, it would appear that there must have been a land connection between Luzon and western Visayan Islands. The fact that we are concerned with subspecifically distinct populations indicates a probable connection in the late Pliocene or early Pleistocene. From what is currently known of the geology and faunistics of the northern Philippines, the most probable connection between the two faunal regions would be across the present Ticao Strait. While there is no geological evidence to indicate the age of the strait, which probably is a dropped fault-block, it is known that there is considerable seismic activity at the present time. I suggest that the Ticao Strait assumed its present topographic attitude during the middle or late Pleistocene.

If I am correct in this assertion at least one heretofore unexplained problem, the fact that Ticao Island includes elements of both the modern Luzon and Visayan faunae, is explained (see discussion of Ticao Island, p. 407). Thus, I assume, a land connection existed between Ticao and Luzon thereby permitting elements of the Luzon fauna to enter the Visayan Islands. However, Ticao was joined to the western Visayans, via Masbate, and that island was joined to the more western islands of Panay and Negros only intermittently.

Palawan Island

Ahaetulla prasina prasina
Aplopeltura boa
Boiga cynodon
Boiga dendrophila multicincta
Boiga drapiezi
Calamaria everetti

Chrysopelea paradisi
Dendrelaphis caudolineatus caudolineatus
Dendrelaphis pictus pictus
**Dryocalamus subannulata*
Dryocalamus tristrigatus
Elaphe erythrura philippina
Gonyosoma oxycephala
Liopeltis philippinus
Liopeltis tricolor
Lycodon aulicus capucinus
Lycodon subcinctus sealei
Maticora intestinalis bilineata
Naja naja miolepis
Natrix chrysarga
Oligodon vertebralis notospilus
Ophiophagus hannah
**Opisthotropis typica*
Psammodynastes pulverulentus
Python reticulatus
Sibynophis bivittatus
Trimeresurus schultzei
Trimeresurus wagleri
Xenopeltis unicolor
Zaocys carinatus

Palawan Island (10° 30.0′ N. Lat., 118° 30.0′ E. Long.) is a rugged, elongate island extending northeast from the northwest coast of Borneo. The island is more than 275 miles long, but only 5 to 30 miles wide. A chain of very rugged mountains, with peaks rising to more than 6000 feet (Mt. Mantalingajan attains an elevation of 6839 feet) extends the length of the island. A very broad, shallow submarine shelf extends to the northeast from the coast of north Borneo. The islands of the Palawan Archipelago, including Balabac, Palawan, and the Calamianes Islands, are all situated on this platform.

The geological history of Palawan is poorly known. Crystalline rocks predominate in the southern portion of the island, while limestones are found in the north. Faunal evidence, however, suggests that during the Pliocene and Pleistocene at least part of Palawan was joined to Borneo, and occasionally to the northern Calamianes Islands.

Thirty species and subspecies of snakes have been found on Palawan. Twenty-three species found on Palawan are taxonomically identical to populations from Borneo. Four Palawan species are known only from the Palawan Archipelago. Of these, three are related to Bornean populations. Only *Trimeresurus schultzei* is of unknown affinities.

Evidence drawn from other groups of animals suggests that Palawan and Borneo are very closely related. Herre (1928, pp. 244–246) and Myers (1951, p. 13) demonstrate very closely that Palawan and Borneo must have

been joined by a subaerial land platform to account for the large number of obligate fresh-water cyprinid fish found there. In a like manner, the amphibians found on Palawan are most similar to Bornean populations.

Panay Island

Ahaetulla prasina preocularis
Calamaria gervaisi iridescens
Calliophis calligaster gemianulis
Dendrelaphis pictus pictus
Elaphe erythrura erythrura
Lycodon aulicus capucinus
Natrix dendrophiops negrosensis
Psammodynastes pulverulentus
Python reticulatus

This island (10° 42.0′ N. Lat., 122° 33.0′ E. Long.) lies to the immediate northwest of Negros to which it is intimately joined by the shallow Visayan submarine shelf. The central highlands attain altitudes of 6726 feet (Mt. Nangtud), 6722 feet (Mt. Malinae), and 5670 feet (Mt. Baloy), and some peaks on the western coasts are almost as high.

The geological history of Panay suggests that the island was partially inundated during the Miocene, Pliocene, and the Pleistocene. Diekerson (1928, p. 90) notes that there may have been two smaller islands during the Pleistocene, rather than one. From a zoological standpoint, however, it is most important to note that geologic and hydrographic evidence both point to a subaerial land connection between Negros, Panay, and, intermittently, Masbate during parts of the Pleistocene.

Panay is one of the least explored of the larger Philippine Islands. Only nine species of snakes have been reported from there; all are known from Negros, and at least three are restricted to those islands and Cebu.

McGregor (1928, p. 199, fig. 50, and pp. 202–203) has shown that the avian fauna of Negros and Panay are practically identical.

Papahang Island

Oligodon meyerinki

Papahang (05° 02.2′ N. Lat., 119° 47.4′ E. Long.) is a small raised coral reef at the south end of the Tawi-Tawi Group between Sanga Sanga and Bongao islands.

The single snake reported from Papahang is widely distributed throughout the southern Sulu Archipelago.

Polillo Island

Ahaetulla grasina preocularis
Boiga angulata

Boiga cynodon
Boiga dendrophila divergens
Calamaria gervaisi polillensis
Calliophis calligaster meclungi
Chrysopelea paradisi
Cyclocorus lineatus lineatus
Dendrelaphis caudolineatus terrificus
Dendrelaphis pictus pictus
Elaphe erythrura erythrura
Hologerrhum philippinum
Lycodon mülleri
Natrix spilogaster
Psammodynastes pulverulentus
Python reticulatus
Trimeresurus flavomaculatus halieus
Zaocys luzonensis

Polillo Island (14° 50.0′ N. Lat., 121° 57.0′ E. Long.) lies about 25 kilometers off the east coast of Luzon. It is separated from that island by a deep channel, the Polillo Strait, which probably resulted from faulting (Dickerson, 1928, p. 115). The island occupies an area of about 297 square miles. Little is known of its geology. It rests upon the broad Camarines submarine shelf and must have been joined to the Camarines Peninsula in the Pleistocene during times of glacial maxima.

A heterogenous assemblage of snakes is present on Polillo. *Natrix spilogaster, Lycodon mülleri, Hologerrhum phillipinum, Cyclocorus l. lineatus,* and *Boiga d. divergens* are typically Luzon species. However, *Dendrelaphis c. terrificus,* the southern subspecies of *D. caudolineatus,* is found on Polillo rather than the Luzon form, *D. c. luzonensis.* Also, *Calamaria g. polillensis* is more closely related to *C. g. hollandi,* the Mindanao subspecies, than to *C. g. gervaisi,* from Luzon (although this similarity may be accounted for by parallel mutations in otherwise similar genetic systems). *Trimeresurus f. halieus* differs only slightly from the typical Luzon form and was probably derived from that population by insular isolation.

The amphibians known from Polillo are, for the most part, related to Luzon populations. A single endemic species, *Cornufer polillensis,* is found on the island. Inger (1954) gives no indication of the affinities of the species.

McGregor (1928, pp. 205–206) includes Polillo in the Luzon faunal district, having shown that the two share a number of endemic genera.

Based on the distribution of snakes, two faunal elements are found on Polillo. The Luzon element predominates. The Mindanao-Samar element is much smaller. The latter may have entered Polillo at a time when the Camarines Peninsula was joined to Samar and was separated from central and northern Luzon. Dickerson (1928, p. 120) has suggested that this occurred during the early and middle Pleistocene. If this be true, then those Mindanao-Samar faunal elements which were able to reach Polillo would

have had an opportunity to become established before the Camarines Peninsula was again joined to Luzon (in late Pleistocene) and the numerically larger and more aggressive Luzon fauna entered that island. This may well account for the presence of *Dendrelaphis c. terrificus* on Polillo, rather than *D. c. luzonensis.*

Samar Island

Ahaetulla prasina preocularis
Boiga dendrophila latifasciata
Calamaria vermiformis grayi
Calliophis calligaster calligaster
Chrysopelea paradisi
Cyclocorus lineatus nuchalis
Dendrelaphis caudolineatus terrificus
Dendrelaphis pictus pictus
Elaphe erythrura erythrura
Lycodon aulicus capucinus
Maticora intestinalis philippina
Naja naja samarensis
Natrix auriculata
Natrix lineata
Oligodon ancorus
Oxyrhabdium modestum
Psammodynastes pulverulentus
Python reticulatus
Stegonotus müllleri
Trimeresurus wagleri

Samar Island (12° 00.0′ N. Lat., 125° 00.0′ E. Long.) lies between Luzon on the north and Mindanao on the south. To the east, and separated by a very narrow channel, is Leyte. The island is the third largest in the Philippines, with more than 5300 square miles of area. There is no distinctive central Cordillera on Samar; the highest point among the relatively low hills rises 2789 feet above sea level. Because of the absence of marked topographic relief, rainfall is fairly evenly distributed over the entire island, which consequently is heavily forested. According to Dickerson (1928, p. 36) the island is a broad marine plain which was uplifted during the late Pleistocene, but it probably was exposed several times earlier in the Pleistocene during times of maximum recession of the seas.

Twenty species and subspecies of snakes are presently recorded from Samar. Of those, nine are found only on Mindanao and related islands, and two (both requiring confirmation) are known on Luzon. The ten remaining species and subspecies are widely distributed throughout the Philippines. There are no endemic species of snakes on Samar.

The amphibian fauna of Samar is not well known. Of the nine species and subspecies known to occur on the island, two are found only on Samar,

Mindanao, Leyte, and Basilan, and six are widely distributed. A single nominal species, *Rhacophorus hecticus*, known only from the type specimen said to have come from Samar, is restricted to that island.

Several genera of both amphibians and snakes, present on Mindanao and Samar, do not enter Luzon. A few genera of amphibians, notably *Bufo*, *Chaperina*, and *Ichthyophis*, are found in Mindanao but not on Samar. In a like manner the snake genus *Aplopeltura* does not reach Samar.

It seems reasonable to conclude that Samar received most of its fauna from Mindanao. The absence of endemic species or subspecies suggests that the fauna entered not earlier than mid-Pleistocene, which is in agreement with what is known of the geological history of the island.

There are two lines of evidence to suggest that Samar was joined to Luzon during the later Pleistocene. For one, as I have already noted above, there are at least two snakes of the Luzon fauna which are presumed to have become established on Samar. These are *Calliophis c. calligaster* and *Oligodon ancorus*. That more Luzon species have not become established on Samar may have been a result of the fact that Mindanao and Samar were joined before Samar and Luzon, and the Mindanao fauna consequently became established and occupied the available habitats thereby preventing successful infiltration by the Luzon fauna.

The second line of evidence for a Samar-Luzon connection has already been discussed (see Polillo Island, p. 402). The fact that several Polillo snakes are more closely related to Mindanao populations rather than to Luzon forms suggests that their progenitors reached Polillo via a Samar-Camarines-Polillo bridge at a time when the Camarines Peninsula was separated from central Luzon during the mid-Pleistocene (Dickerson, 1928, p. 120).

Sibutu Island

Ahaetulla prasina prasina
Oligodon meyerinki

Sibuto (04° 46.4′ N. Lat., 119° 28.8′ E. Long.) is an elongate island, the largest of the Sibutu Group, which lies a few miles off the northeast coast of Borneo. Smith (1924, p. 247) states that the island is a raised coral reef and is flat except for one hill in the center.

Both snakes which have been collected on this island are known from other islands in the Sulu Archipelago and from North Borneo.

Sibuyan Island

Chrysopelea paradisi
Dryophiops philippina

Sibuyan Island (12° 25.0′ N. Lat., 122° 34.0′ E. Long.) lies a few miles

to the east of Tablas and Romblon and is isolated from those islands by a deep channel. Plotting a series of isobath contours around Sibuyan indicates that the sides drop off very precipitously to reach depths in excess of 200 meters. According to Smith (1924, p. 200) the island has but one peak, an old volcanic stock which rises to a height of 6730 feet.

A single specimen of *Dryophiops philippina* has been taken on the island. This snake is known from Luzon and Mindoro, but not elsewhere. *Chrysopelea paradisi* is the only other snake to have been taken on this island. Inger (1954, p. 514) reports one frog from the island, *Rana erythraea*. McGregor (1928, p. 209) suggests that Sibuyan has been separated from all other islands for a very long time or has never been joined to any other island. I am inclined to agree.

Siquijor Island

Chrysopelea paradisi

Siquijor (09° 11.0′ N. Lat., 123° 34.0′ E. Long.) is a small island located off the southeast coast of Negros. It is separated from the surrounding islands, notably Negros, Cebu, Bohol, and Mindanao, by very deep channels, none of which is less than 175 meters deep. McGregor (1928, p. 202) states that the island is of recent origin, though I am unable to find geological evidence either to confirm or to refute that statement.

The single snake reported from Siquijor is widely distributed throughout southeastern Asia. Inger (1954, p. 514) records three frogs from the island, all of which are widely distributed. McGregor (1928, p. 202) states there are three endemic species of birds on Siquijor, but the island lacks a number of species found on neighboring Negros.

There is no clear indication of how the reptiles and amphibians reached Siquijor. The species known from the island could easily have been introduced. Nothing is known about the distribution of other groups of animals on this island. Based on his study of the birds, McGregor believes that it can be grouped with the Negros complex.

Sitanki Island

Dendrelaphis caudolineatus terrificus

This very small island (04° 39.5′ N. Lat., 119° 23.5′ E. Long.), a member of the Sibutu Group, lies within the Tumindao Reef, immediately to the west of the Tumindao Channel and Sibutu Island. Nothing is known of its geology but I suspect that it is a raised coral reef.

The single snake which occurs on Sitanki is a subspecies found in the Philippines as far south as Basilan Island at the north end of the Sulu Archipelago. It has not been taken on any of the Sulu islands and I doubt that it occurs there. It is most likely that the snake was accidentally introduced.

Tablas Island

Calamaria gervaisi gervaisi
Cyclocorus lineatus lineatus
Oligodon modestum

This island (12° 23.5′ N. Lat., 122° 02.0′ E. Long.) lies off the north coast of Panay and southeast of Mindoro. It is a long island with a north-south oriented series of mountains, the highest of which attains an elevation of 2165 feet. At the present time Tablas, and its immediate neighbor, Romblon, which together lie on a shallow submarine shelf, is separated from both Mindoro and Panay by channels exceeding 150 meters depth. There is no evidence to indicate that Tablas has been connected to either island, or to Luzon or Marinduque which lie to the north. Furthermore, there are extensive limestone deposits on the island suggesting marine planation perhaps in the late Pleistocene.

The known snake fauna of Tablas includes three snakes. *Calamaria g. gervaisi* occurs on Mindoro and Luzon; *Cyclocorus l. lineatus* on Luzon, Mindoro, and Negros; and *Oligodon modestum* on Negros, Luzon, and Mindanao. The latter species is best known on Negros, the other localities needing confirmation.

The frogs known from Tablas are all widely distributed species. From this and the above it seems probable that Tablas was populated by animals which arrived by rafting or other fortuitous means during very recent times.

Tawi-Tawi Island

Oligodon meyerinki
Python reticulatus

Tawi-Tawi (05° 11.5′ N. Lat., 120° 02.0′ E. Long.) is the largest island in the Tawi-Tawi Group. It is about 34 miles long by 6 to 14 miles wide and occupies an area of 229 square miles. According to Smith (1924, pp. 246–247) the island is composed mostly of sedimentary rocks, but Corby (1951, pp. 308–309) remarks on the abundance of serpentines and the presence of reef limestones along the northwest coast. I have already remarked on the hydrographic position of the Tawi-Tawi Group (see p. 381).

The two snakes known from Tawi-Tawi are well known from elsewhere in the southern Sulu Islands and in North Borneo.

Ticao Island

Dendrelaphis caudolineatus luzonensis

Ticao (12° 31.0′ N. Lat., 123° 42.0′ E. Long.) lies off the extreme southwest coast of southern Luzon between Luzon and Masbate. The island, which is 129 square miles in area, is separated from both Luzon and Masbate by

deep channels. It is thought to have been joined with Masbate until late Pleistocene when vertical faulting produced the present graben separating the two islands. At the present time Ticao is connected with Masbate near the southern end of the island by a shallow submarine bridge, a part of the Visayan submarine shelf (Dickerson, 1928, pp. 113–114). There is no evidence to indicate the age of the Ticao straits. Before that graben had been formed Ticao may have been joined to Luzon, for reasons already given (see discussion of Negros Island, p. 398).

A single snake has been taken on Ticao Island. It seems noteworthy that this snake is a subspecies found elsewhere only on Luzon and Mindoro. There is no good evidence of a land connection between Ticao and Luzon during either Pliocene or Pleistocene although I have already indicated that the islands may have been joined at one time. McGregor (1928, p. 202) points out that Ticao, based on the distribution of birds, must be associated with the Visayan Islands. He does note, however, that some elements have "infiltrated" from Luzon.

INTERISLAND RELATIONSHIPS

From the preceding discussions, the following generalizations of the interisland relations may be proposed:

I. Luzon, Mindoro, Polillo, Marinduque, and the northern Batan and Camiguin islands form a logical faunal unit. Although Mindoro probably was joined to Palawan in the past, there are no Palawan elements in its herpetofauna. The reptiles and amphibians on Mindoro are clearly related to Luzon. The northern Batan and Camiguin islands, while they have not been joined to Luzon directly, nevertheless have received their fauna from that island, albeit by fortuitous means. Both Polillo and Catanduanes islands were joined to Luzon and their faunal relations clearly associate them with that island. This "Luzon" complex may be characterized by a number of "index" species, including among others: *Oligodon ancorus, Calliophis c. calligaster*[4], *Hologerrhum philippinum, Lycodon mülleri, Natrix spilogaster, Natrix d. barbouri,* and *Naja n. philippinensis.* Some, but not all, of these species are found on all the islands, with the exception of Luzon where they are all present. Nonetheless, two or more of the species are found on each island mentioned and are not found elsewhere in the Philippine Archipelago.

II. Panay, Negros, Cebu, Masbata, Bantayan, and probably Ticao and Siquijor islands form a faunal unit. Negros and Panay are particularly closely associated. Cebu, which received elements of the Negros-Panay fauna probably in the late Pleistocene, was before then an isolated series of raised

4. *Calliophis c. mcclungi,* from Polillo, differs from the nominate form in its lower ventral count. The color pattern is almost identical to the Luzon subspecies. On the other hand, *C. c. gemianulis* from the western Visayan islands has a very distinct color pattern.

coralline islets. These islands rest upon the shallow Visayan submarine platform which lies at depths of less than 50 meters.

Calliophis c. gemianulis, Calamaria g. iridescens, Natrix d. negrosensis, Oxyrhabdium l. visayanum are subspecies restricted to this general area. A number of species of *Pseudorabdion* are presently known only from Negros. However, the other islands of the western Visayan complex have not been as well studied as Negros and populations of *Pseudorabdion,* related to those on Negros, may yet be found elsewhere.

III. Samar, Leyte, Bohol, Dinagat, Mindanao, and Basilan are closely related. Bohol rests upon a shallow submarine shelf which joins it to Leyte. In a like manner Leyte and Samar are connected to Mindanao, by way of Dinagat, by a similar submarine platform. Basilan is separated from the Zamboanga Peninsula by a narrow and shallow channel of water. A drop in sea level of less than 20 meters would give rise to a continuous land mass extending from southern Basilan to northern Samar.

The islands listed here are characterized by several distinctive species and subspecies of snakes found nowhere else. These include: *Boiga d. latifasciata, Calamaria g. hollandi, Calamaria v. grayi, Cyclocorus l. nuchalis, Lycodon dumerili, Naja n. samarensis, Natrix auriculata, Natrix d. dendrophiops, Ntrix lineata, Oxyrhabdium modestum,* and *Stenogonotus mülleri.* Some, but not all, of the species and subspecies listed above occur on all the islands of the Mindanao complex. Basilan shares the greatest number of endemics with Mindanao, a total of eight, while Samar, Leyte, and Bohol, taken in combination, share seven (all known on Samar, five known from Leyte, and four from Bohol). Only two typically Luzon species, *Calliophis c. calligaster* and *Oligodon ancorus,* have been reported from Samar, but both need confirmation.

At least six species which occur on Mindanao have not been reported on other islands. These include *Calamaria mearnsi, Calamaria zamboangensis, Oligodon maculatus, Opisthotropis alcalai, Pseudorabdion ater,* and *Pseudorabdion taylori.* With the exception of *O. maculatus* they are secretive snakes. The affinities of *C. mearnsi* are not known. *Calamaria zamboangensis* may be conspecific with *C. brachyura* from Borneo. *Oligodon maculatus* is probably related to *O. annulifer* and *O. bipartita* from north Borneo. The relationship of *P. ater* are uncertain, but may be intermediate between *P. longiceps,* from western Indonesia and Malaya, and *P. oxycephalum* from Negros. *Pseudorabdion taylori* is probably related to the Bornean species *P. albonuchalis* and *P. Saravacensis.* And *O. alcalai* is close to *O. typica* from Borneo.

The fauna of none of the islands associated here with Mindanao has been collected as thoroughly as that of this island. All are much smaller, although Samar and Leyte are certainly large enough to support highly variable faunas. The faunas of Samar and Leyte are poorly known. For example, up

to the time of this report, only five species and subspecies of snakes had been recorded for Samar Island; nineteen species and subspecies are now known. Future collecting will probably turn up additional species of snakes, most of which, I suspect, will have Mindanao affinities.

An additional factor must also be considered when comparing the total number of species shared between islands of a single faunal unit. Geological evidence suggests that Samar was, until the Pleistocene, covered by water. Mindanao, on the other hand, has not been completely inundated, at least since the Miocene, although many of the present large river valleys were drowned during parts of the Pleistocene. It is evident that the present fauna of Samar is of recent origin while Mindanao's fauna is older. It follows then that there has not been sufficient time for Samar to receive and to accommodate all the possible species and subspecies of snakes which are known to inhabit Mindanao, even assuming that ecological diversification and available habitats are as great on Samar as on Mindanao (which they are not!).

IV. The islands of the Sulu Archipelago, which extend from northeastern Borneo to, but not including, Basilan, form a single faunal unit. The largest of these islands, Jolo, supports the greatest number of species and subspecies. Most of the islands in the archipelago are either recently raised coral ridges or small volcanoes. Faunal elements from both Mindanao and Borneo may be identified on these islands, especially on Jolo.

A single species, *Oligodon meyerinki*, may be thought to characterize this group of islands. Of the thirteen snakes known from Jolo, one is endemic (*Calamaria joloensis*) and of uncertain affinities, two (*Ahaetulla p. praecularis* and *Trimeresurus f. flavomaculatus*) have Philippine affinities, and two (*Maticora i. suluensis* and *Oligodon meyerinki*) are mostly closely related to Bornean species. It seems clear that the Sulu Archipelago has not only provided a migration route for the Bornean fauna into the Philippines, but also has been used by Philippine faunal elements to disperse southward.

It is not surprising that elements of the Philippine fauna have not become established in Borneo as have elements of the Bornean fauna become established in the Philippines. Competition between the numerically large Bornean fauna and the smaller, closely related Philippine fauna would lead to the extinction of the latter.

The Sulu Archipelago, then, is a transitional region having a small fauna of which a part is Bornean and a part is Philippinean.

V. The Palawan Archipelago, including Balabac, Palawan, and the islands of the Calamianes Group belong to the Bornean faunal province. A few old endemic species are found on these islands, most especially the discoglossid frog *Barbourula,* and the snake *Oligodon perkinsi.* Twenty-five of the thirty-one species known from this Archipelago are identical to species known from Borneo. Of the six treated here as distinct species or subspecies, all but two are closely related to Bornean populations: *Sibynophis bivittatus*

is probably only subspecifically distinct from *S. gemiantus; Liopeltis philippina*, which occurs on both Culion and northern Palawan, was probably derived from a population of *L. tricolor* which had been isolated on Culion Island, but which recently has re-entered Palawan; *Oligodon c. notospilus* is distinguished from the typical Bornean population by its lower ventral count; and *Maticori i bilineata* is distinguished by small differences in color pattern. Only *Oligodon perkinsi*, a species known from two specimens from Culion Island, and *Trimeresurus schultzei*, from Palawan, are of uncertain affinities and cannot be related to Bornean species.

ORIGIN OF THE PHILIPPINE SNAKE FAUNA

It is clearly evident that the Philippine snake fauna has been derived from western Indonesia and Malaya. Contrary to previously expressed views (Taylor, 1928, pp. 233–239), there are no genera or species of Philippine snakes which show affinity with strictly Taiwan, Papuan, or Celebesian genera.

Taylor (1928, p. 233) suggested a Taiwan origin for the Philippine species of *Calliophis* (formerly *Hemibungarus*) on the assumption that this genus was not known from the Indo-Malayan region. However, the genus is represented in Indonesia by a single species, *C. gracilis*. I have no doubt that *Calliophis* entered the Philippines a long time ago for the species which occurs there is very distinct. In addition, the genus has a disjunct distribution, with a number of very distinct species occurring at isolated places throughout the Oriental Region.

Although there is considerable floral evidence to suggest an early Tertiary connection of the northern Philippines with Taiwan (Merrill, 1928, pp. 157–166), there are no Taiwan reptile or amphibian elements in the Philippine fauna. Nor, indeed, are there any strictly Philippine amphibian or reptile elements in Taiwan.

Inger (1954, p. 492) has shown that the evidence for a Celebesian dispersal route for Philippine Amphibia is very weak. Insofar as the snakes are concerned, only two species of Philippine snakes, *Dendrelaphis c. terrificus* and *Elaphe erythrura*, have been identified in the Celebes. The latter species has been recorded from throughout the Philippines, including Palawan, and I suspect it will eventually be found in Borneo unless it has become extinct on that island because of competition with more aggressive Malayan species (*e.g., Elaphe melanura*). *Dendrelaphis c. terrificus* is not known from Borneo, although a closely related subspecies occurs there. I suspect that that snake was introduced into the Celebes by natives in the course of their local activities. I find it almost inconceivable that that snake could have entered the Philippines from the Celebes, or vice versa, without some other elements of the fauna also moving from one place to the other. At

least 63 species of snakes are known from the Celebes. Of this number only 15 species are identical to species in the Philippines and of these, 13 are widely distributed throughout southeastern Asia.

Taylor (1928, p. 233) suggested that the snake genus *Stegonotus* had been derived from a Papuan ancestor because the genus was thought to be best developed in that region. There are eight species of lycodontine snakes in the Papuan region which have been assigned to the genus *Stegonotus* but which are more closely related to recognized species of *Lycodon*. The genus *Stegonotus* is a primitive lycodontine snake, and rather than being derived from the more highly specialized Papuan forms, I believe it is a relic of the ancestral stock from which the modern lycodontine snakes were derived. In my opinion, the Papuan lycodontine snakes were derived from the modern Asian lycodontine snakes. In support of this view, I would like to point out that the genus *Dinodon*, which is now restricted to the periphery of the Oriental Region in western and central China is closely related to *Stegonotus*. It, too, probably represents a relic of the early ancestral lycodontine stock.

Excluding Taiwan, the Papuan region and the Celebes as potential sources of the Philippine snake fauna, there remains only western Indonesia and Malaya to be considered. As I have pointed out earlier, with the exception of the genera *Myersophis Oxyrhabdium, Cyclocorus,* and *Hologerrhum,* all the genera of Philippine snakes are found in Borneo. This includes the genus *Stegonotus,* for which I have recently reported a specimen from the Mt. Kina Balu region of North Borneo (Leviton, in press). *Cyclocorus* and *Hologerrhum,* which I suspect are congeneric, may have originated in the Philippines, while *Oxyrhabdium* is an isolated relic whose closest relative lives in the Western Ghats of India.

SUMMARY

Eighty-seven species and subspecies of terrestrial snakes are now recognized in the Philippine Islands. Of this number, 58 species and subspecies (67 per cent) are endemic to those islands. All but four genera and their six included species and subspecies have present-day Indo-Malayan affinities.

Based on the distribution of the terrestrial snakes it is reasonable to suggest that the Philippines be divided into five faunal districts. Each district is characterized by several distinct endemic species which are found nowhere else in the Archipelago:

I. The Luzon district includes the islands of Luzon, Mindoro, Polillo, Catanduanes, Marinduque, and the northern Batan and Camiguin groups. These latter groups have not been joined to Luzon, but nonetheless they have received their small fauna from Luzon.

II. The western Visayan district includes the islands of Panay, Negros, Cebu, Masbate, Bantayan, and perhaps Ticao and Siquijor. Although there

is considerable controversy about the placement of Cebu, I believe the fact that all the snakes known from the island are identical to populations known from Negros, clearly relates the two.

III. Samar, Leyte, Bohol, Dinagat, Mindanao, and Basilan are placed in the Mindanao district. These islands have been joined in the past when the extensive "Mindanao submarine platform" was exposed to subaerial erosion during the Pleistocene.

IV. The Sulu district is a transitional region. Elements of both Philippine and Bornean species, although few in number, have been found here. The small size of the existing islands, and periodic inundation of many of them, probably accounts for the scarcity of animal life (excepting Jolo). The present series of small disconnected islands rests upon a shallow submarine shelf which must have been exposed in the past to subaerial erosion and must have provided the main route of dispersal of Malayan faunal elements into the Philippines.

V. The Palawan faunal district is, in fact, a dismembered part of the Bornean faunal district. The snake fauna of the Palawan Archipelago is nearly identical to that of Borneo. There is evidence to indicate that Palawan may have been temporarily joined to Mindoro in the past. However, the snake fauna is quite dissimilar, suggesting that these islands must have been connected before Mindoro and Luzon were joined.

There is nothing in the snake fauna to indicate that any of the modern Philippine snakes were derived from Taiwan, the Papuan region, or the Celebes. Genera formerly thought to have been derived from one or the other of these areas have Malayan affinities.

LITERATURE CITED

Alcala, Angel C.

1955. Observations on the life history and ecology of *Rana erythraea* Schlegel, on Negros Island, Philippines. *Silliman Journal*, vol. 2, pp. 175–192.

1962. Breeding behavior and early development of frogs of Negros, Philippine Islands. *Copeia*, 1962, pp. 679–726.

Alcala, A. C., and Walter C. Brown

1956. Early life history of two Philippine frogs with notes on deposition of eggs. *Herpetologica*, vol. 12, pp. 241–246.

1957. Discovery of frog *Cornufer guentheri* on Negros Island, Philippines, with observations on its life history. *Herpetologica*, vol. 13, pp. 182–184.

Bemmelman, R. W. van

1949. The geology of Indonesia. Volume 1A, General geology of Indonesia and adjacent archipelagos. The Hague, xxiii + 732 pp.

Boettger, Oskar

1890. [List of reptiles and batrachians from Leyte, Philippine Islands, sent in by Dr. Fr. von Moellendorff.] Berichte der Senckenbergischen Naturforschenden Gesselschaft, 1890, p. lxiii.

Brown, Walter C.

1956. A revision of the genus *Brachymeles* (Scincidae), with descriptions of new species and subspecies. *Breviora*, no. 54, 19 pp.

Brown, Walter C., and Angel C. Alcala

1955. Observations on amphibians of the Mount Halcon and Mount Canlaon areas, Philippine Islands. *Silliman Journal*, vol. 2, pp. 93–102.

1956. A review of the Philippine lizards of the genus *Lygosoma (Leiolopisma)*. *Occasional Papers of the Natural History Museum of Stanford University*, no. 3, 10 pp.

1961. Populations of amphibians and reptiles in the submontane forests of Cuernos de Negros, Philippine Islands. *Ecology*, vol. 42, pp. 628–636.

1962. A new lizard of the genus Gekko from the Philippine Islands. *Proceedings of the Biological Society of Washington*, vol. 75, pp. 67–70.

Brown, Walter C., and Alan E. Leviton

1961. Discovery of the snake genus *Opisthotropis* in the Philippine Islands, with description of a new species. *Occasional Papers of the Natural History Museum of Stanford University*, no. 8, 5 pp.

Brown, Walter C., and Alfredo Y. Reyes

1956. Observations on the incubation period and on hatchlings of several oviparous species of Philippine lizards. *Silliman Journal*, vol. 3, pp. 139–143.

Cooke, Rev. A. H.

1892. On the geographical distribution of the Land-Mollusca of the Philippine Islands, and their relations to the Mollusca of the neighboring groups. *Proceedings of Zoological Society of London*, 1892, pp. 447–469.

Corby, Grant W., *et alii*

1951. Geology and oil possibilities of the Philippines. *Technical Bulletin 21, Department of Agriculture and Natural Resources, Manila*, 363 pp., 57 pls.

Darlington, Philip J., Jr.

1957. Zoogeography: the geographical distribution of animals. New York, xi + 675 pp.

Dammerman, K. W.

1948. The fauna of Krakatau. *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen, Afd. Natuurkunde*, vol. 44, ix + 594 pp., 11 pls.

Dickerson, Roy E.

1924. Tertiary paleography of the Philippines. *Philippine Journal of Science*, vol. 25, pp. 11–48, pls. 1–4.

1928a. Introduction. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 21–30.

1928b. Tertiary and Quaternary palaeogeography of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 76–96.

1928c. Hydrography of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 97–122.

1928d. Mammals of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 273–280.

Dickerson, Roy E.—Cont.

1941. Mollengraaf River: a drowned Pleistocene stream and other Asian evidences bearing upon the lowering of sea level during the Ice Age. *In:* Shiftings of sea floors and coast lines. University of Pennsylvania Bicentennial Conference, pp. 13–30.

Dickenson, Roy E., *et alii*

1928. Distribution of Life in the Philippines. *Monograph 21. Bureau of Science.* Manila, 322 pp., 41 pls.

Duellman, William E.

1958. A monographic study of the colubrid snake genus *Leptodeira*. *Bulletin of the American Museum of Natural History*. vol. 114, pp. 1–152, pls. 1–31.

Herre, Albert W.

1928. True fresh-water fishes of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 242–247.

Huxley, Thomas H.

1868. On the classification of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London*, 1868, pp. 294–319.

Irving, Earl M.

1952. Geological history and petroleum possibilities of the Philippines. *Bulletin of the American Association of Petroleum Geologists*, vol. 36, pp. 437–476.

Inger, Robert F.

1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana: Zoology*, vol. 33, pp. 181–531.

1958a. A note on the Philippine frogs related to *Rana macrodon*. *Fieldiana: Zoology*, vol. 39, pp. 253–255.

1958b. A new gecko of the genus *Cyrtodactylus* with a key to the species from Borneo and the Philippine Islands. *Sarawak Museum Journal*, vol. 8, pp. 261–264, pl. 26.

1960a. Notes on toads of the genus *Pelophryne*. *Fieldiana: Zoology*, vol. 39, pp. 415–418.

1960b. A review of the Oriental toads of the genus *Ansonia* Stoliczka. *Fieldiana: Zoology*, vol. 39, pp. 473–503.

Leviton, Alan E.

1952. A new Philippine snake of the genus *Calamaria*. *Journal of the Washington Academy of Sciences*, vol. 42, pp. 239–240.

1955a. New distributional records for Philippine amphibians. *Copeia*, 1955, p. 258.

1955b. Systematic notes on the Asian snake *Lycodon subcinctus*. *Philippine Journal of Science*, vol. 84, pp. 195–203.

1958. A review of the Philippine snakes of the genus *Oxyrhabdium* (Serpentes: Colubridae). *Wasmann Journal of Biology*, 1957, vol. 15, pp. 285–303.

1959. Systematics and zoogeography of Philippine snakes. Stanford University (Ph.D. dissertation), xx + 865 pp. [Abstract published in Dissertation Abstracts, 1960, p. 4467.]

1961a. Description of a new subspecies of the Philippine snake *Dendrelaphis caudolineatus*. *Occasional Papers of the Natural History Museum of Stanford University*, no. 9, 7 pp.

LEVITON, ALAN E.—Cont.

1961b. Keys to the dangerously venomous terrestrial snakes of the Philippine Islands. *Silliman Journal*, vol. 8, pp. 98–106.

1963. Contribution to a review of Philippine snakes, I. The snakes of the genus *Oligodon*. *Philippine Journal of Science*, vol. 91, pp. 459–484.

LEVITON, ALAN E., and WALTER C. BROWN

1959. A review of the snakes of the genus *Pseudorabdion* with remarks on the status of the genera *Agrophis* and *Typhlogeophis* (Serpentes: Colubridae). *Proceedings of the California Academy of Sciences*, ser. 4, vol. 29, pp. 475–508.

MAYR, ERNST

1944. Wallace's line in the light of recent zoogeographic studies. *Quarterly Review of Biology*, vol. 19, pp. 1–14.

MCGREGOR, RICHARD C.

1928. Birds of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 168–213.

MERRILL, ELMER D.

1928. Flora of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 130–167.

MYERS, GEORGE S.

1951. Fresh-water fishes and East Indian zoogeography. *Stanford Ichthyological Bulletin*, vol. 4, pp. 11–21.

1953. Ability of amphibians to cross sea barriers, with especial reference to Pacific zoogeography. *Proceedings of the Seventh Pacific Science Congress*, vol. 4, pp. 19–27.

SCHULTZE, WILLY

1928. Insects of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 248–266.

SMITH, WARREN D.

1924. Geology and mineral resources of the Philippine Islands. *Monograph of the Bureau of Science*, Manila, no. 19, 559 pp., 39 pls.

TAYLOR, EDWARD H.

1922a. The snakes of the Philippine Islands. *Monograph of the Bureau of Science*, Manila, no. 16, 312 pp., 37 pls.

1922b. Additions to the herpetological fauna of the Philippine Islands. I. *Philippine Journal of Science*, sec. D., vol. 21, pp. 161–204.

1923. Additions to the herpetological fauna of the Philippine Islands. III. *Philippine Journal of Science*, vol. 22, pp. 515–555.

1928. Amphibians, lizards and snakes of the Philippines. *In:* Dickerson, R., *et alii*, 1928 (which see), pp. 214–241, pls. 27–32.

UMBGROVE, J. H. F.

1938. Geological history of the East Indies. *Bulletin of the American Association of Petroleum Geology*, vol. 22, pp. 1–70, 1 pl.